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STENOTHERMY AND ZONE-INVASION[1]

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THE conception of geographical distribution seems to have come to the botanists of the later fifteenth and earlier portions of the sixteenth centuries as a distinct and gradually developing idea. They began to realize that the plants of central and northern Europe were different from those of Greece and Italy as treated of by Theophrastus and his successors and were worthy of study for their own sakes. With the revival of learning, the discovery of the "New World" and the attention paid to the plants and animals of the different countries being made known through the visits of the various voyagers, both the knowledge of the different countries and that of the natural objects brought back from them emphasized more and more the idea of geographical differences in flora and fauna and the gradual perception that there might be some general laws or principles governing them. It remained for Humboldt in a series of papers in 1805, 1807, 1816, 1817 and 1820, to place the matter of the geographical distribution of plants on a firm scientific basis. After Humboldt's preliminary work, came the studies of a number of leading botanists and gradually there have arisen various points of view, especially as to factors concerned and as to the division of the subject into various categories according to the special factor, or set of factors, emphasized. The studies in ecology, which have come more recently to represent the activities

[1] Annual lecture before the Barnard Botanical Club, New York City, delivered March 12, 1920.

toward solutions of the problems of distribution, are founded more particularly on the influence and control of distribution by edaphic factors, or those more particularly connected with the substratum and concerned in the studies of association and formations, in other words having to do particularly with topographic distribution as contrasted with climatic distribution.

Humboldt's publications concerned themselves particularly with climatic distribution, although, incidentally, he necessarily touched upon topographical distribution. The chief factor of control in climatic distribution recognized by Humboldt and his successors is temperature, and Humboldt called attention, in most graphic ways, to the resemblances between the climatic zones of latitude over the earth's surface and those of altitude passed through in the ascent from sea-level to thousands of meters above it. Those of us who are older remember the reproductions of Humboldt's diagrams of the various zones (or perhaps better, belts) of vegetation of mountain peaks situate in different latitudinal zones which were reproduced in the various atlases and older geographies. Lamouroux, in 1825 and 1826, applied the general principles of Humboldt, DeCandolle and Robert Brown, to marine plants, especially to the algæ, and distinguished latitudinal zones and differences of distribution in depth (belts), as well as the effect of certain factors on topographical distribution. Lamouroux was followed by Greville and Harvey in the attempts to discuss the distribution of marine algæ and the latter (1852) divided the Atlantic coast of North America into 4 divisions and emphasized the position of Cape Cod as a demarcation point. These authors and their ideas may be taken as starting points of the discussions more or less contemporaneous and later.

A definite attempt to determine the criteria of a climatic zone was made by C. Hart Merriam (1894, 1898) in his papers on "life-zones" and "crop-zones" of the United States. Merriam used summation indices compiled for a large number of stations and divided the

country into life-zones in accordance with the indices thus obtained. Merriam also shows that, by plotting the isotherms of 18°, 22°, and 26° C., for the six hottest weeks of the year, divisions are separated from one another corresponding in all essential details to those obtained by plotting summation lines. This is practically the method I have used in separating climatic zones of the surface waters of the oceans. Livingston and Livingston (1913) have discussed the system of Merriam and proposed a system of efficiency temperature coefficients which are claimed to represent something more of the basic principles of physiology upon which the final explanations of distribution should be based. A comparison between isoclimatic lines plotted for the United States on the direct summation basis and isoclimatic lines plotted on the efficiency indices basis shows a strong, but not absolute tendency toward agreement. The Livingstons, however, do not discuss the interpretation of their charts as regards plant distribution in detail.

Nearly 30 years ago, while attempting to obtain some idea of the temperature relations of the geographical distribution of the Laminariaceæ, I noticed a seemingly definite relation to the lines of mean maxima (summer lines or isotheres) of surface temperatures. Some brief remarks on these relations were published in 1893. Farther studies seemed to emphasize the relation between the 10, 15, 20, and 25 degree (Centigrade) isotheres or lines of mean monthly maxima and the limits of distribution of various floral groups, and in 1914 I read a paper at the Twenty-fifth Anniversary Celebration of the Missouri Botanical Garden (published 1915) as a preliminary communication on the temperature relation of the distribution of the marine algæ as expressed in terms of mean monthly maxima and minima (isotheres and isocrymes). In this paper, I made a tentative division of the surface waters of the oceans, etc., into zones according to the courses of the 10°, 15°, 20°, and 25° C. isotheres, and announced that a rough tabulation indicated that the great majority of species are confined to one or

another of these zones, that a considerable number of species extend over two of these zones, that a comparatively small number are found to extend over three zones, while the number credited with extending over four or five zones are extremely few and almost always doubtfully so accredited. It was also suggested that the disturbance of zonal distribution, so far as the occurrence is concerned, is probably due to spot distribution, *i.e.*, where waters of a higher or lower temperature than that of the zone in which they are placed exist due to local physical conditions, and to seasonal lowering of the temperature normal to the zone. In 1916, in another address (published 1917), I reasserted these statements and added something as to the significance of the isocrymal lines, or lines of monthly mean minima. I suggest using the latter lines to divide the zones into proper provinces.

Since writing the last paper I have investigated the floras of the coast of New England and have found that the species may be readily arranged in two categories, one of the colder waters (20° C. or less) and the other of the warmer waters (20° C. or over), and while some of these are found only north of Cape Cod and others only south of Cape Cod, the majority are found on both sides of the cape, which is, however, the natural dividing point and approximating closely to the position of the 20° C. isothere. The separation is made by ascertaining whether a given species of the last group in particular inhabits warmer localities to the north or is found only in cold localities or appears or fruits only in the colder season to the south. Similar examinations of other, but less perfectly known floras, add to the conviction that species of marine algæ, at least, are normal to only one zone of 5° C. amplitude as to mean maxima, except in the cases of those of the very coldest waters and it may be that they are no exceptions to such a rule. Furthermore, it may be assumed, from observing the isotheres and isocrymes in favorable portions of the surface waters of the oceans, viz., those undisturbed by the larger ocean

currents, that the normal, or at least the minimum seasonal variation in temperature is closely approximating to 5° C. This, added to the amplitude of 5° C. mean maximum variation, makes the normal amplitude of temperature within each zone about 10° C. and the temperature interval favorable to the persistence of a species within a given area, so far as active growth is concerned, is very little, if any, over 10° C. The seasonal range in some portions of the surface waters of the oceans may amount to as much as 18° or 20° C. In such localities as may have such an extreme range of temperature, we may, I think, assume that a condition of quiescence, or rigor, may exist, at least in the perennial species, such as exists in the case of perennial plants in zones on land where there is an alternation of a frost with a frostless season, as it does particularly in the polar and most of the so-called temperate regions.

It will appear from a careful consideration of what I have been saying, that the temperatures for normal persistence of any particular species of marine plant lie within narrow limits, although many marine plants are credited with extending over fairly wide ranges of temperature. We are, consequently, brought directly to a consideration of the ideas implied in the use of the terms stenothermal and eurythermal. The proposal of these terms, or rather their equivalents in German, rests with Karl Moebius who, in 1877, published a paper in *Die Natur* on the external factors of life of marine animals. According to Moebius the eurythermal animals can endure wide ranges of temperature and continue their occupation of extensive zones and range in depth because they are able to reproduce under such conditions. It is this conception of being able to reproduce at widely separated temperature limits that I wish to call particular attention in order that I may discuss it later. Moebius states that the eurythermal animals are much less numerous than those which normally occur and withstand a narrow range of temperature which he calls stenothermal animals. The latter seem to be the more

usual type and this agrees with what I have found in my attempts to tabulate the marine algæ as I have already mentioned with emphasis. To repeat the idea of Moebius, in a rather free translation of his own words, eurythermal animals are those which in the surface waters of the temperate zones are able to exist and to continue their kind through reproduction under all of the various temperature relationships of the different seasons of the year.

The terms eurythermal and stenothermal have not come into any noticeable use in botany and are not widespread even in zoological literature, although they are very convenient. They are both to be found in the later editions of Webster's and in the supplement to the Century Dictionary. They are discussed in the latest edition of the Encyclopedia Britannica by G. H. Fowler, under the article on "Plankton." Fowler says: "In relation to temperature the wide-ranging species are termed eurythermal, the limited stenothermal (Moebius); the terms are useful to record fact, but not explanatory. It seems to be the case that to every organism is assigned a minimum temperature below which it dies, a maximum temperature above which it dies and an optimum temperature at which it thrives best; but these have to be studied separately for every species." The definitions of Moebius and the comments of Fowler are exactly to the purpose of our consideration, since the one is from the purely distributional point of view expressing a fact only, while the other seeks to link the fact with some explanation, preferably physiological. Our own discussion of these terms and the underlying conceptions must necessarily proceed on a somewhat middle course, largely from the distributional point of view, but with such regard for the interpretation of the physiological basis as may be possible from our present knowledge.

It will be of the greatest assistance, I think, to consider some concrete cases of eurythermal species and to inquire into the conditions of their continued persistence

under different temperatures. One constituent of the marine flora of the northern hemisphere which has interested me very much indeed, is the common eel-grass, *Zostera marina,* a marine spermatophyte. As commonly regarded as to specific limits, this plant extends from the northern coasts of Europe down along the western coast and enters the Mediterranean Sea, occurring spotwise in the northwestern portion of it and being represented also in the northern Adriatic. *Zostera marina* is represented in one or two localities in southwestern Greenland and, reappearing at the Strait of Belleisle, it seems fairly continuous in its distribution thence down to the coast of North Carolina, at least, and is reported from West Florida and the Bermuda Islands, although I can not make certain as to whether it actually grows in either of the last mentioned stations. *Zostera marina* is reported from both the North American and the Asiatic coasts of the North Pacific, but the exact limits of its occupancy of these shores is in doubt. The greatest range of temperature experienced by the *Zostera* is that on the Atlantic coast of North America, where it extends from waters of a mean maximum of 0° C. to those of a mean maximum of somewhat over 25° C. It is also found in localities where the seasonal temperature range of the surface waters is from somewhat below 0° C. to 15° C. It ranges through all the temperature zones of surface waters from the Upper Boreal (0°–10° C.) to the Tropical (25°–30° C.), *i.e.,* five zones in all. I shall discuss the reasons for this wide extension of the range of *Zostera marina* later, but desire to call attention here to the facts that we are dealing with a perennial plant with unusually effective methods of vegetative multiplication and devices for wide dispersal.

Another eurythermal marine species is *Ascophyllum nodosum,* one of the bladder-bearing Fucaceæ or Rockweeds. On the Atlantic coast of North America, this species is found in some abundance from well up on the west coast of Greenland down to the northeastern coast of New Jersey, or on coasts having a range of mean

maximum temperature from 0° C. or below to about 22° C. and seasonal ranges of about 17° C. maximum. *Ascophyllum nodosum* is also a perennial species. *Rhodochorton Rothii* is a delicate red alga which, nevertheless, seems to be a perennial and *Monostroma Grevillei* a membranous green alga, and *Polysiphonia urceolata,* a filamentous red alga, are annuals, but with the same range as *Ascophyllum nodosum. Grinnellia americana* is the last example of many eurythermal algæ of the Atlantic coast of North America I desire to bring forward. It is a strikingly beautiful annual membranous red alga and extends from northern New England (North Temperate Zone, 15°–20° C., mean max.) to the coast of North Carolina (Tropical Zone, 25°–30° C., mean max.). Other examples of eurythermal species might be given, but those I have mentioned are typical and reasonably well known. They will serve as a good representative basis for discussion with the idea in mind that what is indicated by the eurythermy of one and another of them will, by analogy, also seem extremely possible to be the case with all other types and individual species extending over ranges of temperature of more than 10° C.

Stenothermal species are particularly characteristic of the Tropical Zone, in very few portions of which the seasonal variation in temperature is over 10° C. Species confined to the Upper Boreal or to the Upper Austral Zones are also narrowly stenothermal, since the entire range of temperature in these zones is not over 10° C. The temperate and subtropical zones are usually sufficiently affected by seasonal changes to show a range of temperature greater than 10° C., but in the southern hemisphere in particular, there are portions of these zones, at least, that show only a 10° C. range and consequently may possess stenothermal species. The annual species of any particular zone, and even perhaps all annual species, are stenothermal so far as their actively vital processes are concerned, but may endure temperatures of more extended range in the resting seed or spore condition. This naturally brings us to inquire as to the

nature of the fundamental differences between the eurythermal and the stenothermal species, and this, in turn, is closely connected, as I shall hope to make plain, with the second topic of this paper, viz., zone-invasion.

I have already tried to make clear the fact that my investigations have tended very strongly to convince me that each and every species of marine plant is normal to only one zone, and that, when a species is credited to, or found to occur in, two zones, it is normal to only one of them and is to be found in the other because for some reason it finds in the second zone the temperature conditions, both as to degree of temperature and as to duration of that degree of temperature, of the zone to which it is normal. In a similar fashion, if a species is found to inhabit three, four, or even five zones of different temperature relations, it is possible to make certain that it is normal to only one of these and invades the other zones because it finds the proper temperature conditions for its continuous existence. The proper temperature seems certainly to be that which is most intimately connected with reproduction, since it is this function that is most necessary to persistence in the particular locality. In the laboratory, under controlled conditions, algæ, in particular, have been found to be very sensitive to even slight changes of temperature, as Ewart (1896) has demonstrated. It does not seem as if the same algæ, in their ordinary environment, could be thus sensitive as West and West (1898) have held, but Ewart (1898) has answered their objections, claiming that, in nature, they are probably equally sensitive, but withstand seemingly great changes for reasons that prevent these changes actuating. This is something of the truth in the case of species invading colder from warmer, or warmer from colder zones in that they find in the invaded zones the temperatures, both as to intensity and duration, which are favorable to their growth and reproduction and which are the same as they find normally in their proper zone.

Zone-invasions proceed in one of two directions, or,

occasionally, in both. They may proceed from warmer to colder zones, they may proceed from colder to warmer zones, or they may proceed from a zone of intermediate temperatures to both colder and warmer zones. Where warmer spots or areas exist in the midst of cooler waters, species of warmer zones may exist spotwise in the cooler zone. Where certain portions of the waters of a warmer zone are depressed in temperature by cold currents or upwellings, or, for certain seasons of the year, suffer a general lowering of the temperature, there and then may species from cooler zones be expected to put in an appearance. The extent of such invasions will depend naturally upon the intensity and duration of the unusual temperature. A consideration of the examples I mentioned as typically eurythermal may serve to make this idea more clear.

Zostera marina seems, on careful study of its occurrence and habits on all the coasts where it is found, to be normal to the North Temperate Zone with the mean maxima for the hottest month from 15° to 20° C. If this is the case, we are dealing with a species which extends in both directions from its normal zone. The more northern extensions may be explained by the fact that the very shallow and protected lagoons and interiors of prolonged and narrow bays preferred by this species may have the temperature of their waters raised through the action of the air and of the sun. In such waters, insolation undoubtedly is the most effective agent in raising the temperature as much as 10°–12° C. or even higher. To the south, the invasions of *Zostera marina* may be assumed to be made possible by the seasonal lowering of the temperature of the waters through the lower winter temperatures, *e.g.*, the winter temperatures on the coast of North Carolina is somewhat under 20° C. and the winter temperature on the coast of West Florida is also somewhat under 20° C. It would be expected, if the seasonal lowering of the waters south of the lower limits of the North Temperate Zone allows the eel-grass to find its normal temperature for fruiting in an earlier

season of the year than late summer, that the farther south the species grows, the earlier will be the fruiting season. Unfortunately, it is impossible to obtain any extensive data on this subject, but reliable testimony indicates that it flowers and fruits somewhat over a month earlier on the coast of New Jersey than it does on the coast of northern New England. It seems therefore that the critical temperature for persistence of this species, at least through flowering and seeding, is the same throughout its limits and that the species does not differ from a typical stenothermal species from this point of view. *Zostera marina,* however, is one of the most typical of the eurythermal species in that it must endure extremes of both heat and cold in various portions of its extensive range and in the various seasons of the year in each and every portion of its habitat. It is not known as to the temperature limits of the vital activity of the vegetative portions of the *Zostera,* but it does not seem possible that their separation can possibly be as wide as the differences between the extreme limits of the temperatures of endurance and probably are very much less. The *Zostera* probably has rather narrow limits to the temperature range of its vegetative activities and undoubtedly passes into a resting or hibernating condition, a condition of cold-rigor or of heat-rigor as the case may be, at the upper as well as at the lower portions of its temperature range. The land perennials of temperate zones do this and it seems safe to assume that *Zostera* does the same.

The case of *Ascophyllum nodosum,* a perennial brown alga of complex structure, is a very excellent one for study. This species ranges from the western coast of Greenland to that of New Jersey and it has a similar range on the northern and western European coast. On the coast of Greenland, it fruits in summer and it fruits earlier and earlier in the season as it proceeds towards the south, until, in the region of Long Island Sound, it fruits in late winter and early spring. The frond, or

vegetative portion, of *Ascophyllum* does not seem at all vigorous during the summer of the southern portion of its range. It seems perfectly evident that *Ascophyllum* is normal to the Upper Boreal Zone and invades the zones to the south because it finds, even on the northeastern coast of New Jersey, seasonal temperatures of proper duration below 10° C. The isocryme, or winter isotherm, of 5° C. touches the coast of New Jersey at about the point that marks the southern limit of the range of *Ascophyllum nodosum.* We have in this species, then, a eurythermal species whose critical temperature and amplitude for persistence range from 0° to 10° C. and which undoubtedly passes into a condition of heat rigor during the hotter months of the year in the southern portion of its range. It differs from the last example, in that its course of invasion is in one direction, viz., to the south.

Rhodochorton Rothii is a very delicate, filamentous, perennial red alga of very lowly stature. It has a range very similar to that of the last species and, in the southern portions of its range, fruits only in winter. The same things may be said of this species as were said of *Ascophyllum. Rhodochorton,* however, is a shade or cave plant in the more southern portions of its range, seeking the cooler portions of the warmer districts. This is doubtless its only opportunity of surviving the heat and is of great benefit to its delicate structure.

Monostroma Grevillei and *Polysiphonia urceolata* are annuals, with about the same range as the last two. They are summer annuals in the waters of Greenland, but are winter and early spring annuals of the southern portions of their range. With the exception, then, of the temperatures endured by their resting spores, they are confined to the temperature range of the Upper Boreal Zone and are practically stenothermal.

The last example quoted is *Grinnelia americana,* an annual red alga, apparently normal to the Long Island Sound district and therefore of the North Subtropical

Zone (20°–25° C.). North of Cape Cod, it is to be found only in certain warm protected spots where the insolation is sufficient to raise the temperature to that of the subtropical zones while the waters outside are those of the temperate zones. To the south of the North Subtropical Zone the species is a winter annual and follows the 20° C. isocryme. *Grinnelia* is, therefore, a stenothermal and not a typical eurythermal species and invades both colder and warmer zones, the colder because of warm spots and the warmer because of favorable seasonal conditions.

Farlow, in his Marine Algæ of New England, has amply explained still a different type of invasion, viz., from a colder zone into a warmer and I have some additional details in a paper soon to be published. The *Laminariaceæ*, or kelps, a number of species of perennial red algæ, some other browns, greens, reds, etc., pass Cape Cod and are to be found in the colder waters which are usually the deeper waters to the south of it. This seems to be an invasion from the North Temperate into the North Subtropical. It does not mean, however, as is the case also with the examples I have mentioned and discussed, that these seeming invaders are living in waters of a different range of temperature from that of the normal zone. Their eurythermy is but seeming, at least so far as this particular invasion is concerned.

In conclusion, I may say simply this: stenothermy is the rule both from the point of view of distribution and of physiology, at least so far as effective reproduction is concerned; eurythermy is largely, if not entirely, a matter of endurance of a wide range of temperature, much of which endurance is due to the power to enter into a condition of rigor after certain extremes of temperature of either direction are passed; and a study of the various reasons for zone invasion assists greatly in making these facts apparent.

PHYLOGENY OF THE ARTHROPODA WITH ESPECIAL REFERENCE TO THE TRILOBITES[1]

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THE phylogeny of the Arthropoda has been discussed so often that merely to summarize previous opinions would require an article of considerable length. In a recent number of the NATURALIST,[2] Professor Crampton has reviewed the subject from the standpoint of a student of insects, the most specialized Arthropoda. It may be of interest to see what results are reached when approached from the point of view of a student of the trilobites, the most ancient members of the phylum. The characteristics of trilobites may be summarized as follows:

APPENDAGES

During the last two years I have had occasion to restudy practically all of the known specimens of trilobites whose appendages are preserved. The limbs of twelve species, representing nine genera, are now more or less fully known. Those which leave least to be desired are *Neolenus* from the Middle Cambrian, *Triarthrus, Calymene, Ceraurus,* and *Cryptolithus* from the Middle Ordovician, and *Isotelus* from the Upper Ordovician. Representatives of all three of the orders into which the class is divided are included in this list, which contains examples of both "primitive" and "specialized" trilobites.

The appendages of all these genera, with the exception of *Isotelus,* whose exopodites are still unknown, prove to be constructed on one plan. An articulatory segment

[1] This is an abstract of a more extensive discussion of the affinities of the trilobites now being published by the Connecticut Academy of Arts and Sciences.

[2] AMERICAN NATURALIST, Vol. 52, 1919, p. 143.

(coxopodite) supports the proximal ends of two branches, an ambulatory endopodite and a setiferous respiratory exopodite. The endopodite consists in all cases of six segments, the terminal one with movable spines on the distal end, usually three in number, but occasionally several. The proximal segment of the endopodite is a basipodite and gives rise to the exopodite, although both branches articulate with the coxopodite. The method of articulation of coxopodite, exopodite, and basipodite is similar to that of the second thoracic limb of the recent *Anaspides,* as figured by Calman. The exopodite is in all cases composed of a flattened shaft, along the posterior margin of which are delicate flattened setæ. The form of articulation of the basipodite, exopodite, and coxopodite indicates that when one of the outer branches moved the other accompanied it, but as the exopodites were always above the endopodites, they appear to have been of comparatively little use in swimming, and were probably chiefly respiratory organs.

All of the trilobites mentioned, so far as their state of preservation will allow determination, have four pairs of limbs of this sort on the cephalon, a pair on each segment of the thorax, and as many pairs on the pygidial shield as there are annulations on its axial lobe. In front of the biramous limbs there is one pair of uniramous, richly segmented, tactile antennules. The ventral membrane of the trilobite was very thin and feebly supported, so that the articulation of the limbs was not with it, but with infoldings of the dorsal shell which extended downward beneath the glabeller and dorsal furrows. The distal end of each of these appendifers fitted into a notch in the upper side of the corresponding coxopodite. A projection of this latter segment extended mesally nearly to the median line, forming endobases which on the cephalon, and usually along the whole of the body, functioned as food-getting organs.

No other parts of the limbs have yet been found, although I have searched diligently through all of the

known material preserving the ventral anatomy. Therefore it seems to me that Walcott has not sufficient evidence for the structures he illustrates and describes as epipodites and exites in *Neolenus,* epipodites in *Triarthrus, Calymene,* and *Ceraurus,* and spiral gills in the last two.[3] The presence of none of these things can, in my view, be proved.

There is little modification of the appendages of different parts of the body. The gnathobases of the coxopodites on the cephalon of *Triarthrus* are more jaw-like than those on the remainder of the body, and in the same species the segments of the endopodites of the pygidium and posterior part of the thorax are more triangular than those of the anterior ones. *Cryptolithus* has the thoracic legs bowed backward to form more efficient pushing organs, and in all species with long hypostomata the anterior biramous appendages seem to be more or less degenerate. Thus, *Calymene* appears to have two pairs of very delicate biramous appendages back of the antennules, and the first one or two pairs of gnathobases of *Calymene, Ceraurus* and *Neolenus* seem to be somewhat reduced, but there is no evidence that any pair of appendages is entirely lost. All the evidence seems to indicate that Beecher correctly homologized the cephalic appendages with the antennules, antennæ, mandibles, maxillulæ, and maxillæ of the Crustacea.

FORM OF BODY

Trilobites are always depressed, flattened animals, with a broad head composed of at least five fused segments, a thorax of from two to forty-four free segments, and a pygidium made up of a variable number of undifferentiated segments. The anal opening is at the posterior end of the pygidium, and the growing point just in front of it, as in other arthropods. New segments are introduced into the posterior end of the pygidium during moults, are pushed forward by the introduction of others

[3] Smithsonian Misc. Coll., 1918, Vol. 67, No. 4.

behind, and eventually a certain number are freed from the anterior end of the pygidium to form the thorax. Trilobites with an elongate worm-like form have numerous thoracic segments and small pygidia, while many others have few free segments and the pygidium nearly as large as the cephalon. These latter have usually been called more specialized than the former, but it is obvious from the method of introduction of new thoracic segments that the reverse is the case. This opinion is confirmed by a study of the ontogeny, for it is found that in the protaspis the pygidium of any species is proportionally larger than at any later period in life, and that many species pass through a stage in which they are isopygous.

There is a certain amount of evidence that the pygidium was used as a swimming fin, and some species seem to have had sufficiently strong muscles to enable the animal to dart away suddenly when attacked. Trilobites with large pygidia would thus have a certain advantage over the others, and, as a matter of fact, it was this type which persisted longest. The broad depressed body was not as well adapted for a nectic mode of life as a compressed fishlike one would have been, but it is the form which could most easily be kept afloat and propelled with the minimum of effort. The young of all species are circular or broadly oval in outline, and those adults with subequal shields depart least from that form. A fair inference from the above would be that the elongate crawling trilobite was more specialized than the isopygous swimming one.

Internal Anatomy

Naturally knowledge of the internal anatomy is not as full as could be desired, but what follows appears to be based on reasonably clear evidence.

The mouth is ventral and usually situated back of the middle of the cephalon. Its position depends upon the length of the "upper lip" or hypostoma, and in extreme cases may be at the posterior end of the cephalon. There

is evidence from ontogeny and phylogeny of a backward migration of the mouth, coincident with the same movement of the eyes. In both cases this is probably due to the enlargement of the anterior end of the mid-gut. From the mouth the esophagus extends upward and forward to the enlarged mesenteron which occupies the greater part of the large cavity between the hypostoma and glabella. The intestinal canal tapers backward, but no differentiation of the posterior portion has yet been made out. The anus is beneath the posterior end of the axial lobe. The heart is elongate, chambered, branchiopod-like, and in the one species in which it is preserved, extended from the middle of the cephalon to the anterior end of the pygidium. The principal muscles were a dorsal pair of extensors, attached at the posterior margin of the cephalon and anterior ring of the pygidium, and a ventral pair of flexors, both with branches inserted in each segment. All of these organs were within the axial lobe.

COMPARISON WITH OTHER ARTHROPODA

Having thus briefly stated the principal characteristics of the trilobites, the method will be to indicate briefly the similarities which exist between the trilobites and other arthropods, and to show that there is nothing about the bodily form or characteristics of the appendages to negate the possibility of a derivation directly or indirectly of all other classes from that under discussion. It is obvious that in this short paper each class can be treated but briefly.

CRUSTACEA

The trilobites are themselves crustaceans, as is amply proved by their biramous appendages. An attempt will be made to show that they may have been ancestral to the other crustaceans.

In recent years it has been generally considered that the Branchiopoda were more nearly allied to the trilobites than any other living animals. Bernard, the chief

proponent of this association, did not consider either subclass derivable from the other. Walcott has more recently stated that the trilobites were derived from the branchiopods and in this has been followed by Crampton. The points of relationship are: in both subclasses the number of segments is not fixed, and in both there are some species which have large numbers of them; both have a well-developed labrum (hypostoma); both have functional gnathobases along the body; the change in metamorphosis of the branchiopod is comparatively small, although *Apus* is by means a "grown up nauplius," as Bernard put it.

So far as these similarities are important, they do show a close relationship of the two groups, but none of them indicates that either is more primitive than the other. When a closer comparison is made, it at once becomes evident that the trilobites are much more primitive than the branchiopods. For example: trilobites have no carapace; some branchiopods do; trilobites have serially similar appendages on all segments, branchiopods have very different appendages on the head from those on the thorax, and some of the abdominal segments lack them entirely; trilobites have antennæ like the other cephalic and trunk appendages, branchiopods have the antennæ highly modified, degenerate, or absent. In other words, branchiopods are in all these respects much more specialized than the trilobites. Finally, the limbs may be considered. Lankester has shown that the schizopodal limb of the higher Crustacea may be explained as derived from one like that of the thorax of *Apus,* and most students of the Crustacea have followed him in considering the phyllopodous limb the most primitive among the Crustacea. This theory has now been completely upset, for Walcott has found several undoubted branchiopods with appendages in the Middle Cambrian, and the best preserved of them (*Burgessia*) show that the limbs were not phyllopodan, but like those of trilobites. The ancient branchiopods having had simple trilobite-like limbs, it

can no longer be held that phyllopodan limbs are primitive, and, stripped of their trilobite-like disguise, these wormlike crustaceans may no longer be considered most primitive. The possession of biramous limbs by the branchiopods of the Middle Cambrian, added to their other undoubted likenesses, indicates the possibility that they were derived from the trilobites, although some of them had then already attained the specialized carapace, pedunculate eyes, and limbless hind-body. This possibility is converted into strong probability when one considers the structure of the beautiful *Marrella splendens* Walcott. The head of this "lace-crab" of the Middle Cambrian is obviously highly specialized, but the structure as a whole proves it to occupy an intermediate position between the trilobites and more specialized crustaceans, including the branchiopods. It resembles the higher crustaceans in having the antennæ uniramous, in lacking exopodites on the cephalic appendages, gnathobases on those of the thorax, and in the absence of pleural lobes from the test of the trunk. This animal retains enough characteristics of the trilobites to show that it was derived from them, and has attained enough characteristics of the higher Crustacea to show that it belongs with them. A better connecting link can hardly be expected.

The Copepoda prove, on analysis, to be much more closely allied to the trilobites than had been supposed. All students have remarked upon the many primitive features of the non-parasitic members of this group, but have generally explained them by the sweeping assertion that they must be degenerate. Why, if they are degenrate, do the Copepoda show fewer modifications during development than any other Crustacea except the trilobites? They, instead of *Apus,* represent the "grown up nauplius."

These animals resemble the trilobites in lacking a carapace, in possessing pleural lobes, which, however, are incurved instead of being flattened. The greatest resem-

blances are, however, in the appendages. All these, except the antennules, maxillæ, and maxillipeds, are biramous, the antennæ and mandibles being especially like those of trilobites. The Copepoda are easily derivable from the latter, even though there are no fossil forms to connect the two groups. Since they lack compound eyes, and show very slight evidence of having ever possessed them, it is even conceivable that they branched off from the Hypoparia, the most primitive of trilobites.

The Ostracoda and Cirripedia are of course highly modified by their somewhat peculiar method of life, but when the young are studied, the characteristics of trilobites are readily observed. In fact, it is really surprising that the trilobite-like character of the crustacean nauplius is so consistently ignored. It has a broad depressed form like a trilobite. It has simple antennules, biramous antennæ, and mandibles like a trilobite, and the gnathobases of the last two function as mouth-organs. An hypostoma is present, and there is a growing point, as is evidenced by the way new segments are added. It is not, it is true, a trilobite, but it looks like a trilobite modified by suppression, and taken in connection with other evidence, certainly does no injury to the theory that the higher Crustacea were derived from the trilobites.

The Malacostraca can be mentioned but briefly. Their most ancient representative whose appendages are known, *Hymenocaris* from the Middle Cambrian of British Columbia, had biramous appendages like those of the trilobites, and most of the modern members of the group have similar ones on some part of the body. As in lower crustaceans, when the exopodites are lost or degenerate, epipodites are developed to replace them, and thus the limbs become variously modified. It is remarkable, however, how close a resemblance there is between the appendages of a trilobite and those of fresh-water syncarids from Tasmania, and even in the Decapoda the seven segments of the walking leg are serially homologous with the seven segments of that of the trilobite. It

has frequently been objected to the trilobites as ancestors of the Crustacea, that they had wide pleural extensions and a large pygidium. To the first it may now be replied that some trilobites did get rid of the pleural extensions, but that, on the other hand, most Crustacea retain some remnants of them. I have already shown above that the large pygidium in trilobites was more primitive than the trunk with numerous free segments, and it may further be pointed out that some orders of Isopoda do have a pygidium.

ARACHNIDA

My task in this class is rendered somewhat easier by the fact that the followers of Lankester appear to have accepted his explanation of the descent of the class from the trilobites. While I agree with the general thesis, I must point out that a certain amount of caution must be used, for the connecting links are not nearly so satisfactory as one would like them to be, and the trilobites are not nearly so closely related even to the Merostomata, as they are to the higher Crustacea.

In the first place, while the Trilobita were probably the ancestors of the Arachnida, they do not themselves belong to that class. Lankester advanced six reasons for placing them in the Arachnida, but the first is the only one having any considerable weight, and is the only one which will be discussed here. This point was that they had only one pair, apart from the eyes, of pre-oral appendages, while the Crustacea have two pairs. Researches since Lankester's article was written seem to show that this apparent difference between the Arachnida and Crustacea is not fundamental, for the cheliceræ of the former are probably to be homologized with the antennæ, not the antennules of the latter, so that the mouth is in the same position in relation to the appendages in both groups. Further, the mouth does not occupy a constant position in the trilobites, but with the elongation of the hypostoma, is pushed backward, so that from one to four pairs of appendages may be attached in front of it.

If dorsal tests only be considered, one can pick out an excellent series showing gradations from a trilobite into *Limulus*. Thus, there are in the Middle and Upper Cambrian the Aglaspidæ, with *Limulus*-like head, trilobite-like free thoracïc segments, and *Limulus*-like telson. Following the history of the group through the Paleozoic, there is, in the Silurian, *Neolimulus* with a head which is surely that of *Limulus* but which has vestigial facial sutures, and free thoracic segments are present. By Devonian times, the thorax had begun to fuse into a shield, although some of the Pennsylvanian species retained a few free segments at the anterior end of the thorax. This series is so convincing that one must believe that the Xiphosura developed from the trilobites, but a study of the appendages shows that there are greater differences between those of a trilobite and *Limulus* than between those of a trilobite and one of the highest Crustacea.

The greatest difference is in the complete lack, at any stage of development, of the antennules, from which it follows that the anterior shield in the Xiphosura is a cephalothorax in which at least seven segments are incorporated. It is, of course, entirely possible that in one line of evolution of the trilobites the antennules were lost and the antennæ developed as cheliceræ, but if the test be applied to the Aglaspidæ, the results are at variance with the expectation. Walcott has found Aglaspidæ with appendages in the Middle Cambrian, and they seem to have five pairs of appendages on the cephalon, two pairs of which are elongate, multi-segmented, tactile antennæ, and biramous appendages are present on the thorax.[4] These animals were still Crustacea, and the development of elongate antennæ instead of cheliceræ shows that they were not tending in the direction of the Xiphosura. It is possible, however, that when the appendages of more Aglaspidæ are known, it will be found that some of them showed a tendency to lose the antennules and develop cheliceræ.

[4] Smithsonian Miscl. Coll., Vol. 57, No. 6, 1912.

Some progress has been made toward the connection of the trilobites with the Merostomata, as the Limulava of Walcott are, in a certain sense, intermediate between the two. The Limulava are, however, true crustaceans, for they have five pairs of cephalic appendages, the first of which are elongate uniramous antennules, and also biramous, trilobite-like limbs on the anterior part of the thorax. They are especially trilobite-like in the fact that the antennæ are not elongate tactile organs, but, in *Emeraldella* at least, are biramous. The relationship to the Merostomata is expressed in the shape of the head, body and telson, and the grouping of the cephalic appendages about the mouth. If these animals lost the antennules, developed the antennæ into cheliceræ, added two thoracic segments to the cephalon, modified the appendages, and added a sternal operculum, a merostome would be produced. I think it is obvious that to change a trilobite into a marine arachnid is a more complicated process than to change one into a crustacean of any kind.

To compare the spiders directly with the trilobites may seem somewhat fanciful, yet in some respects the spiders are more trilobite-like than *Limulus* is. On the germ band there is a pair of buds in front of the mouth which probably are antennules. These later fuse to form the rostrum, and the cheliceræ move into a pre-oral position. Moreover, Jaworowski has shown that the pedipalps on the germ band of *Trochosa singoriensis* are biramous. In young spiders the abdomen is segmented, and the anterior segments bear pairs of limb-buds, some of which are later lost, while others develop into lung-books or spinnerets. The number of abdominal segments appears to be variable, from eight to fourteen, another feature which suggests the trilobites. The spiders very probably did not spring directly from this group, but will eventually be traced to it, and not through the Xiphosura.

Insecta

I quite agree with Crampton that Handlirsch has presented little or no evidence that the Insecta were derived directly from the trilobites. His chief point was that the most ancient known insects, the Palæodictyoptera, were amphibious, and that their larvae, which lived in water, were very like the adult. His second was that the wings of the Palæodictyoptera probably worked up and down only, and that the two main wings were homlogous with rudimentary winglike outgrowths on each segment of the body. These outgrowths resemble the pleural lobes of trilobites, and were considered to have been derived from them. Comstock, who has recently reviewed the question, does not see any evidence that the Palæodictyoptera were amphibious, and I do not think any entomologist or paleontologist has accepted the idea of a direct transformation of pleural extensions of segments of trilobites into wings. The "para-notal" theory certainly does not involve any such conception. That the insects are derived indirectly from the trilobites is, however, entirely possible, and Professor Crampton has marshalled the data for one such possible line of derivation through the Crustacea in the article to which allusion was made in the opening sentences of this essay. Another theory is that advanced by Tothill, who suggested that the Insecta arose through some chilopod-like tracheate, rather than directly from a marine organism. Tothill[5] has pointed out that in the germ band, spiracles appear as early as the limb-buds, and may thus indicate a tracheate ancestor for the insects. This is, of course, discounting the possible effect of acceleration on the embryo, but the whole anatomy of the insects indicates long separation from the marine ancestor. The germ band of the chilopod is somewhat more primitive than that of the insect, for in some species both antennules and antennæ are present, and the maxillæ and first maxillipeds are biramous. The

[5] *Am. Jour. Sci.*, Vol. 42, 1916, p. 373.

presence of two pairs of antennae does not point directly to the trilobites, but to some offshoot like *Marrella,* and it is possible that the line has been: trilobite, *Marrella*-like marine animal, chilopod-like tracheate, insect.

There remain only the Diplopoda, which show a few trilobite-like characteristics, notably their lateral outgrowths and the endopodite-like walking legs on every segment. Antennules are present, antennæ absent, mandibles and maxillulæ much modified, the latter possibly biramous, and maxillæ absent. The most characteristic feature, the possession of two pairs of limbs on each segment on a part of the trunk, can be shown to have arisen comparatively recently (geologically), for Silurian and Devonian fossils which are undoubted diplopods have a test like that of a trilobite and eyes much like those of a *Phacops.* While there are no close connections, there is nothing to show that the Diplopoda could not have been derived from the Trilobita.

SUMMARY

After the above survey, it should appear that the trilobites, particularly in respect to their appendages, are more primitive than any other Arthropoda. The chief modifications in other groups are in the nature of reductions, in the loss of whole appendages, of branches or of segments. Extra segments are sometimes added in certain appendages, and new outgrowths, epipodites, are common among the Crustacea. The trilobites have what seems, at first sight, a peculiar and specialized dorsal test, but now that it has been shown that the pleural lobes may be lost and the pygidium reduced to a single segment, and, chiefly, that the wormlike form is not primitive but secondary, they may be viewed in an entirely new light.

In the oldest fossiliferous rocks, Lower Cambrian, trilobites are plentiful, branchiopods rare, and no other arthropods present. A greater differentiation is seen in the Middle Cambrian fauna, due, however, entirely to the

remarkable assemblage found by Walcott at a single locality in British Columbia. In this fauna the Crustacea are represented by trilobites, anostracan and notostracan branchiopods, *Marrella,* Limulava (possible ancestors of the merostomes), Aglaspidæ (possible ancestors of the Xiphosura), and Leptostraca, the most primitive Malacostraca. The Upper Cambrian brought the first true Merostomata. In the Ordovician, Ostracoda and Cirripedia first appear, and in the Silurian the first undoubted Xiphosura, primitive Diplopoda, and Scorpiones. Insecta and air-breathing Arachnoidea, including Araneæ, appear suddenly in the Pennsylvanian (Upper Carboniferous), and the oldest known Chilopoda are found with them. All of the tracheates probably have a long pre-Pennsylvanian history, however, and the record of the fossils is liable to be amplified by new discoveries at any time.

The geological record, so far as it is now available, is in favor of the theory that the other Arthropoda were derived from the trilobites, for although Crustacea were highly diversified by the Middle Cambrian, all other than these were rare, and the trilobites, while they had not reached their highest development, were exceedingly abundant and varied.

If the trilobites were the most primitive arthropods, the question of the ancestry of the phylum resolves itself into a search for the progenitors of the former. What would be the form of the animal from which the trilobite was derived? The depressed form universal in the subclass and the equally universal lateral ("pleural") lobes have already been commented upon. From a study of comparative morphology, it appears that the more ancient trilobites, and the more ancient members of higher families within the subclass, have the most nearly flat form, the narrowest axial, and the widest pleural lobes. Turning to ontogeny, it is found that in most cases the protaspis of any species shows the same characteristics. All these suggest a broad depressed animal with narrow

axial portion as the ancestor. Only a few specialized trilobites like the Remopleuridæ and one subfamily of the Cheiruridæ show extensive reduction of the pleural lobes.

A study of the ontogeny of trilobites with both large and small pygidial shields shows that the pygidia are proportionally larger in the protaspis than in the adult, and the more ancient forms pass through a stage in which they are practically isopygous. This suggests that the ancestor had subequal cephalic and abdominal shields. Since the thorax grows by the breaking down of the pygidium, the ancestor should lack free thoracic segments. Curiously enough, among Walcott's remarkable finds in the Middle Cambrian there is an isopygous crustacean without free thoracic segments. It was named *Naraoia* and referred to the Branchiopoda by Walcott,[6] but since it satisfies the theoretical considerations and evidently can not be referred properly to any other subclass, I am inclined to look upon it as the simplest of all trilobites. The specimens so far described are not fully preserved, but the appendages are apparently biramous and trilobite-like, and there are at least three pairs on the head and fourteen on the pygidium. From Agnostidae with subequal shields and two thoracic segments to *Naraoia* with subequal shields and no thoracic segments is but a step. If the pygidium were built up by the coalescence of once free segments, that step would be in the direction of specialization, but since the reverse is the case, the extraordinary conclusion is reached that the simplest trilobite did not look at all like the traditional benthonic round annelid.

The study of the ontogeny of many species of trilobites long ago established the fact that in the ontogeny the eyes, which may be entirely absent in the very young of the simplest oculiferous species, appear first on the anterior margin and during growth move backward on the head. A point which has not been noted is that this movement is correlated with a backward movement of

[6] Smithsonian Miscl. Coll., Vol. 57, No. 6, 1912, p. 175.

the mouth, as indicated by the increase in length of the hypostoma, and an increase in size of the anterior part of the glabella. There is nothing mysterious about the process, as it is probably due to the increase in the size of the anterior (digestive) portion of the "stomach." This indicates that in the ancestral form the mouth and eyes were close to the anterior margin, and does away with the necessity of the bent annelid to explain their migration. Many of the simpler trilobites are of course blind, as is *Naraoia*.

It is true that much of the argument involves the use of principles drawn from the study of ontogeny, but where the ontogeny points to animals which actually exist and helps to explain observed facts, its use seems to be justified. Swinnerton has recently suggested that students of the ontogeny of trilobites have been led into an entirely wrong interpretation because they have not realized that the protaspis, like the nauplius, is a specialized larva adapted to a nektonic mode of life. Since Swinnerton believes that the trilobites are descended from benthonic annelids, one can not but wonder why the nektonic trochophore was not carried over instead of requiring the development of a new and totally different free-swimming larva by the trilobites. All indications derived from the present study are that the primitive trilobites were floating and swimming animals, that their adoption of a crawling habit was a specialization, that the protaspis was nektonic because the adults were, and that the nauplius of recent Crustacea is a similar free-swimming larva because it harks back to ancestral conditions.

THE UTILIZATION OF ECHINODERMS AND OF GASTEROPOD MOLLUSKS

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THE Puget Sound region, in the State of Washington, is noted for the wonderful abundance and diversity of its fauna. The region is also noted for its several groups of archipelagoes, of which the San Juan Archipelago is an especially beautiful one.

Around the shores of these islands, echinoderms are found in great profusion. Particularly noticeable are the common forms of starfish, sea urchins, and sea cucumbers. The most common starfish are *Piaster ochraceus* and *Evasterias troschelli,* which show, respectively, considerable substantive and merestic variation. In the environs of Bremerton, the latter finds more congenial conditions than any of the other common species, and there it occurs in a ratio of 25 to 4 of the former, while in the San Juan island group, *P. ochraceus* is by far the most numerous. Besides these two species, *P. paucispinus* and many others are also found, but in smaller numbers. The twenty-rayed starfish, *Pycnopodia helianthoides,* occurs quite plentifully at various places, *e.g.,* Bremerton, Griffin Bay, East Sound, etc. Sea urchins, *Strongylocentrotus dröbachiensis, S. purpuratus, S. franciscanus* are very numerous, especially the former. At low-water, *S. dröbachiensis* may be seen in the bays of the northern part of the sound in large patches, and at a depth of only four meters. *S. franciscanus,* which becomes very large—7 to 13 centimeters in diameter—is found just below low-water mark; I have seen it in large numbers in the vicinity of the Biological Station at Friday Harbor. The most noticeable species of sea cucumbers are *Cucumaria japonica* (Semper), *C. chrondjelmi* (Theil), and *Stichopus cali-*

fornicus (Stimpson) Edwards. *C. chrondjelmi* is exceedingly abundant near the Sucia Islands. All these species may be obtained by dredging, and *C. japonica* may be picked by hand at low-tide.

Of all the echinoderms, common starfish, *Piaster, Evasterias,* etc., are most easily obtained. They occur within the lower limit of the average ebb-tide, and sometimes in such profusion that, especially when the stars are brightly colored, they may be seen at half a mile's distance. Their occurrence is independent of town sites, being determined by the nature of food available. Shores well supplied with barnacles usually have a large number of starfish. And the fact that they are abundant at a distance from towns adds to the desirability of their use as a food product. The parts of the starfish and sea urchins utilizable as food are the gonads. During the breeding season, these grow enormously, so that in the starfish the body becomes twice its normal size, the gonads completely filling the gastric cavity. The part of the sea cucumber utilizable as food is the muscles.

Echinoderm gonads as a food commodity would be the object of an industry of annual periodicity like the salmon industry. As the spawning season of starfish and sea urchins comes in the spring, the canning of the roe could be well completed before the salmon season begins; or the making of echinoderm gonads into caviar might well be done along with the canning of fish, whether salmon or otherwise. The gonads of the various species of the larger starfish are ripe in April; those of the sea urchin, in June, as regards species of the north Pacific coast (Figs. 1–3).

There can be no question about the advisability of using the spawn and muscles of echinoderm as food, even in a country where all kinds of food are as plentiful as in the United States. The question is rather how to utilize this part of nature's storehouse to the best advantage for mankind.

Barbier (1908) states that the natives of Madagascar

have developed a considerable industry in the utilization of starfish, sea urchins, and sea cucumbers as food. In 1902, the marketable quantity of sea cucumbers represented a value of 175,000 francs. The province of Tulear produced alone 30 tons, but the lack of necessary labor prevented further production that year.

Taylor (1908) reports an interesting fact, namely, that

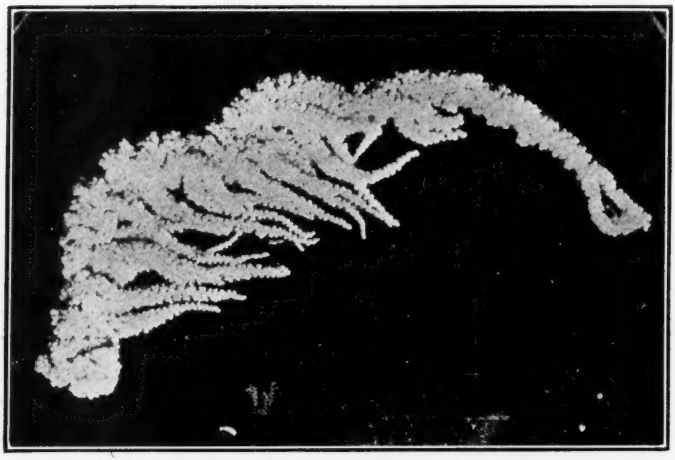

FIG. 1. Mature ovary of *Evasterias troschelii*, ½ natural size. (Photo by author.)

the Arctic Fox of the Aleutian Islands, so highly valued for its beautiful fur, feeds, in winter, on echinoderms, *e.g.*, sea urchins.

Reagan (1907) claims that the sea urchin (*Strongylocentrotus dröbachiensis*) is used by the Pacific coast Indians as food.

In conversation with the United States Commissioner of Fisheries (1916) I learned that the roe of starfish is being used in France as food and also as bait in the sardine fisheries; and through Professor Kincaid, I am informed that certain species of sea urchins, which in the market of Naples are called "Frutta di Mare," and in the West Indies "Sea Eggs," are sold as food, but I have not

had the opportunity to consult literature on these points.

Brunchorst (1898) shows that a number of excellent food fish common to the coast of Norway feed on echinoderms, and mentions especially: *Anarrhichas lupus,* and *A. minor; Lycodes esmarckii; Pleuronectes microcephalus,* and *P. platessa;* others not used as food fish but which feed on echinoderms are, *A. latifrons, P. cynoglossus,* and *Galeus vulgarus.* Perhaps other food fish such as *Gadus callarias* and *G. pollachius* also feed on echinoderms, as I have at least found at times small starfish in their stomachs.

Carr (1907) found that out of 150 starry rays (*Raia radiata*) ten contained echinoderms (*Asterias, Echinus,*

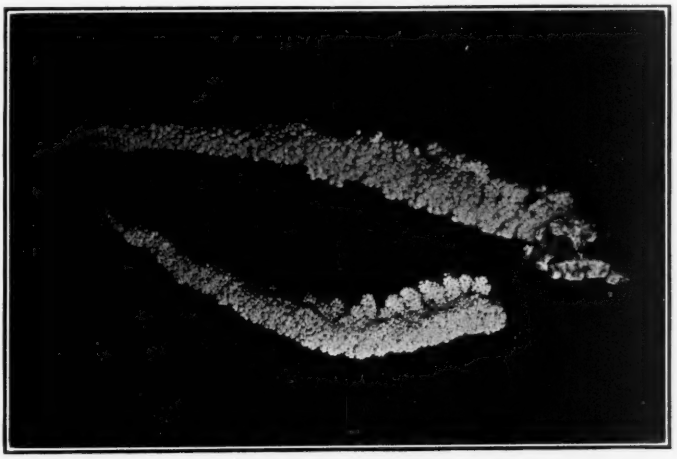

FIG. 2. Semi-mature ovary (largest) and spermary (smallest) of *Plaster pauci-spinus,* $\frac{2}{3}$ natural size. (Photo by author.)

and *Ophiocoma*), and out of 12 haddock (*Gadus æglefinus*) two contained echinoderms (*Ophiocoma*). Three out of 13 wolffish (*Anarrhichas lupus*) contained echinoderms. In 1908, the same author tabulated observations on 370 common dab (*Pleuronectes limanda*) and showed that out of this number, 56 contained echinoderms, *e.g.,* Ophiuroids and Echinoids; 5 long rough dab (*Hippoglossus liman-*

dioides) out of 60 fish contained Ophiuroids; 10 out of 25 *G. æglefinus,* contained echinoderms (Ophiuroids and Echinocyamus), and one gray gurnard (*Trigla gurnardes*) out of 150 fish also contained echinoderms.

From the findings of Brunchorst and Carr it is seen that various kinds of fish feed on echinoderms, whence the suggestion that echinoderms be used as bait. How-

FIG. 3. Mature ovary and spermary of medium-sized twenty-rayed starfish, *Pycnopodia helianthoides,* $\frac{2}{3}$ natural size. (Photo by author.) N.B. The alveoli are larger in the ovary.

ever, it may be that for a number of forms echinoderms are resorted to only when other food is out of reach, though the common dab, according to Carr, appears to eat them during the greater part of the year. The long rough dab feeds less on echinoderms than the common dab, perhaps owing to a difference in migration habits of the two.

A large part of an echinoderm industry would be by-products, since the main bulk of the starfish consists of material best suited for guano. No absolute waste material need remain; all of the animal may be utilized. Indirectly, the shell-fish industries would be benefited by

reducing the number of starfish in regions where shell-fish live, as various forms of starfish feed on marketable shell-fish. Lebour (1916) makes an interesting statement:

> The mussels on this coast have not many enemies, but by far the most important of these is the starfish, *Asterias rubens*, which constantly preys upon them. A formerly flourishing bed near the Tyne has lately been exterminated by this starfish and it is a bad enemy everywhere. *Purpura lapillus* [a small gasteropod] devours the mussels on the scaup, Holy Island, and here in parts the devastation caused by this small and very destructive mollusk is great. It does not, however, appear to be a scourge elsewhere. The only possible way of dealing with such foes would be to destroy all starfish whenever found, and to collect the *Purpura lapillus* systematically, and also its spawn, and destroy both.

Kellogg (1910) records nothing favorable about the starfish. To him it is a pest.

> The removal of these pests has always been a very difficult matter, and no entirely satisfactory method has been devised for accomplishing it.

When the *economic value* of starfish is realized, depletion of starfish may result from overfishing, and "to destroy all starfish whenever found" will be out of the question. If it prove necessary to protect starfish, where only the gonads are to be used, these may be removed on the grounds, while fishing, and the starfish at once put back into the water below low-tide level to avoid unnecessary exposure. The operation of removing the gonads could be carried out successfully without killing the animal, since echinoderms possess great regenerative powers. As male gonads may be unfit for caviar, it is worth noting that they can be easily distinguished from the female since the latter are of pinkish color while the former are of light yellowish hue. The reproductive power, and growth of starfish, are very great. According to Kellogg, "A female starfish may, if large enough [depending on amount of food] begin to extrude eggs during its second summer, and many by that time attain the required size."

As echinoderms, on the north Pacific coast, can be more easily caught than any other kind of sea food, the starfish and some of the sea cucumbers may simply be picked

up at low-tide, and sea urchins and certain sea cucumbers may be obtained by dredging, the expenses connected with their utilization as a whole should be comparatively low,

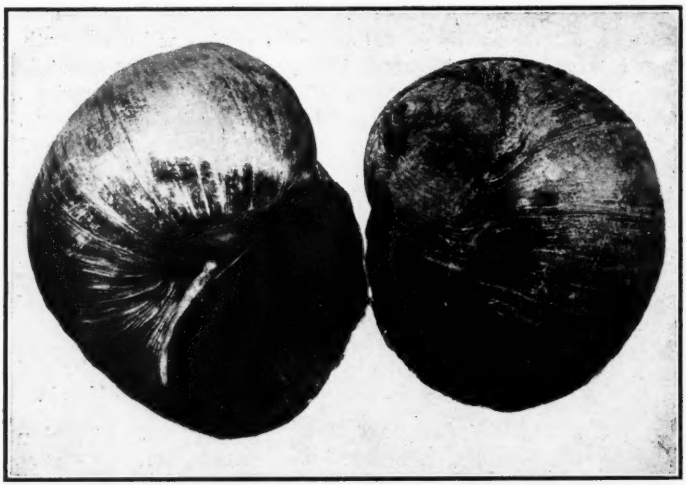

FIG. 4. Live shells of *Polynices lewisii*, natural size. (Photo by author.)

making it possible to sell the products at a reasonable price.

In quoting Lebour, I mentioned *Purpura lapillus* as a destructive enemy of bivalve mollusks. I now wish to point out the possibility of utilizing destructive gasteropods:

Polynices lewisii, a very large gasterpod (Fig. 4), is a great destroyer of mollusks of commercial value. Its foot may reach the length of 21 centimeters and a width of 13 centimeters, and a depth of the body about 10½ centimeters. It destroys oyster beds by its burrowing in them in search of clams, but it is not known whether it attacks oysters directly. On account of its burrowing habits, the oystermen, at the head waters of Puget Sound, destroy large numbers of them.

Keep (1888), speaking of *Lunatia lewisii* Gld., now merged in *Polynices*, claims that it possesses a flint drill

which it carries in its mouth, and by use of which it drills into the clam or whatever mollusk it may encounter, killing the same. This, it is claimed, is a common habit of members of the family Naticidæ of which the genera *Natica* and *Lunatica* are best known. Daugherty (1912) says:

> *Natica* is another drilling sea-snail common to our coast. It burrows in the sand for clams and bores a hole with its radula, rotating its own body in the action.

Agersborg (1918), during the summer of 1916, observed a number of specimens of *Polynices* in the actual act of killing and eating clams. At low-tide, when rowing along the shores of Dyes Inlet near Chico, Washington, a large number of *Polynices* was found. As the tide was very low it was possible to pick them up by using a dip-net. Some of them, however, were not so easily removed from the bottom as others, holding to the same by means of the enormous foot, or having sucked down into the sand to the depth of about ten centimeters, leaving only part of the shell uncovered in the middle of a pit. It was soon found that there was a definite cause for their holding on to the bottom so firmly; these individuals of *Polynices* were feeding. The process of feeding was found to be somewhat different from that described by Keep, and Daugherty.

As *Polynices* crawls along the bottom it kills any clam it encounters by suffocation. The soft-shelled clam, *Mya arenaria,* which is quite numerous in the bays of Puget Sound, is a common victim. Hard-shelled clams, *Paphia staminea, Cardium corbis,* are also an easy prey for this ravener. In the case of *Mya,* the gasteropod sucks itself over the syphon down into the sand until its victim is dead from suffocation, and then when the clam has opened, *Polynices* simply sends its proboscis between the valves and devours the content. As for the hard-shelled clams, the process of feeding is similar to that used when eating a *Mya* but the method of killing is different. In this case the prey is held in the "sole" of the foot until the

adductor muscles are relaxed or the victim is dead, when the feeding begins. Several dead clams, of these species mentioned, were found in possession of *Polynices,* but none of them were drilled. It is thus seen that this gasteropod is very decidedly an enemy of the bivalved mollusks, but its method of killing clams is different from that described by Keep and Daugherty.

Several specimens of *Polynices lewisii* were obtained and brought to Bremerton, where experimentation on the possibility of utilizing them as food was carried out. Two methods of preparing the animals for the table were used: first, steaming in the moisture contained within its swollen foot, and second, breaking the shell and frying the animal alive in butter. Either of these methods gave good results. By the former, a delicious broth was the principal result; by the latter, a large piece of variant meat. The foot, however, by either method, becomes rather tough when cooked. As some one has held that the meat of *Polynices* is poisonous, not so very much was eaten; no ill effects, however, were felt from that consumed. The idea that *Polynices* is unfit for food is of course baseless, as I am informed by Professor Kincaid that thousands of *Polynices* shells may be found in the Indian kitchen-middies, which indicates that the Indians used this mollusk as food, and as the *Polynices'* shells are found in these remains in much greater proportion than any other shells, this gasteropod must have been widely sought by the Aborigines; or it may be that *Polynices* was formerly more abundant than any other mollusk on our western coast. At any rate, this gasteropod seems to have been a common diet of the Indians who lived along Puget Sound. The tastes of Indian and white man are not unlike in these matters, for white people eat various species of clams, also an Indian diet, and seem to delight in such food, as is well demonstrated by the establishment of shell-fish canneries on our coasts.

It does not seem unreasonable, therefore, that *Polynices* as well will find a ready market. In fact, it might

well be prepared as an extra delicacy and sold as such, and in that way made to make up partly for injuries that it inflicts on the bivalve-mollusks.

Barbier (1908) enumerates a large number of gasteropod mollusks used by the natives of Madagascar in various ways. Not only is the animal matter used as food, but the shells are commercialized as well. Having enumerated ten species of the genus *Murex,* and 139 species from different genera including *Littorina, Nerita, Cypræa, Pterocera, Strombus, Neritina, Turbo, Conus, Terebra, Natica, Cassis, Harpa, Mitra, Voluta, Vasum, Oliva, Fasciolaria, Purpura, Rapana, Eburna, Nassa, Ranella, Triton, Fusus, Neptuna, Busycon,* and *Pyrula,* all of which are marine forms, he adds the following terrestrial and freshwater gasteropods: *Helix hæmastoma* L., *Bulimus perversus* L., *Mulimulus multilineatus* Say, *Pupa uva* L., *Clausilia cana* Gld., *Auriculus auris* Midæ L., *Tudora versicolor* Pfr., and *Helicina miltochila* Cross, and says:

> Tous ces coquillages servent à la nourriture des indigènes qui mangent leur chair cuite dans la coquille sur un feu ardent sans acun assaisonnement.

It is worth noting that genus *Purpura* which causes great destruction of the mussel beds on the English coast, and which was suggested by Lebour to be systematically collected and destroyed, serves the Indians of Madagascar as food. *Murex, Natica, Nassa, Busycon,* and others related to the gasteropod types on our coasts are being utilized as food by the natives of Madagascar. *Cycotypus canaliculatus* Verrill & Smith, 1873 (*Busycon canaliculatus* Say, or *Fulgur canaliculata* Gould, 1887, Dall, 1889), is a very pernicious enemy of oysters. According to Sumner, Osburn and Cole, 1908,

> It is abundant in shallower water generally . . . pretty generally distributed throughout Buzzard Bay and Vineyard Sound. It preys upon mollusks and is said to be destructive to oysters (p. 707).

It is still of little commercial value save that of being used for dissecting purposes, and some Europeans, in New

England, have ventured to use it as food, but this is by no means a common practise. The genus *Urosalpinx* is closely allied to *Murex*; several of its species are found on the east coast of the United States. Arnold (1916) says of *Urosalpinx cinerea:*

> This well-known species is regarded by Chesapeake and Long Island Sound oystermen much in the light of a plague. These active predaceous mollusks live upon bivalves, and preferably upon oysters. They bore a small hole through the shell of their helpless victims, and then proceed to extract the succulent, fleshy animal from within. The oystermen call them by the suggestive name of "drill," and wage incessant warfare upon them.

Daugherty claims: "It is a feeder upon oysters;" and Kellogg says in part:

> There are several species of the snails that are destructive to bivalves. Among these the large winkles or conchs of northern shores do very little damage; but some of the smaller forms, particularly the oyster drill, cause large losses here and there along the Atlantic coast. . . . The drill, or *Urosalpinx,* is most destructive to young oysters. It seems to be unable to bore through the shell of large individuals. . . . Like starfish, oyster drills were formerly not numerous on the New England oyster beds, but in recent years have increased greatly. In New York Bay, and in the Chesapeake, they are abundant . . . in Louisiana, a larger drill, *Purpura floridana,* is sometimes very destructive.

Opinions thus seem to vary as to the destructive habits of some of the gasteropods upon bivalve mollusks, but the findings of Dr. Copeland (1916) are very conclusive: *Busycon* reacts positively toward oyster juice, in fact, the oyster often forms a conspicuous part of its natural diet. All the investigators, however, seem to agree about the habits of *Urosalpinx.* In view of the fact that these gasteropods *are* esculent, injurious to other marketable mollusks, near large cities, and generally easily obtained, it seems rather strange that they are seldom found in the market. *Polynices lewisii,* which is still quite abundant in the upper part of Puget Sound, is generally destroyed by the oystermen whenever found in the vicinity of oyster fields. As a natural enemy, *P. lewisii* seems to have none more dangerous than the twenty-rayed starfish (*Pycno-*

podia helianthoides). As a matter of fact, bays that have none or very few *Pycnopodia* may have a large number of *Polynices,* and bays that are well populated with this starfish have remarkably few *Polynices* present. When I later experimented on the sensitivity of *Polynices* to *Pycnopodia* (Agersborg, 1918) I found in all instances, that when the slug came into contact with the star, it withdrew its foot at once. The monstrous foot, though it seemed impossible that it could be withdrawn within the shell, was very quickly covered thereby. Upon withdrawing the foot in a hurry, as it does when in contact with *Pycnopodia,* the periphery of the foot, which is perforated, throws a spray like a garden sprinkler with the holes in the spray-disk plugged except those around the periphery. No matter how much larger the animal is than its shell, when all the water is squeezed out of the foot, the former can be completely covered by the latter. In such a condition, however, *Polynices* can not live very long. It is itself easily exhausted when completely shut up within its shell. If it is not allowed to take in fresh water supply when it comes out to breathe it soon relaxes, an easy prey to the gluttonous *Pycnopodia.* In fact, when leaving *Polynices* with *Pycnopodia* in an aquarium, two of the former were killed and eaten by the latter within three days, leaving the shells and opercula.

The absence of *Polynices* where *Pycnopodia* abounds, together with the facts observed when keeping the two in the same aquarium, seems to indicate definitely that *Pycnopodia* preys on *Polynices.* As mentioned above, *Polynices* is a nuisance to oyster growers, even if it does not feed on oysters, for it destroys the oyster beds by burrowing in them; primarily *Pycnopodia* is a gasteropod feeder, and though it is quite omnivorous and may feed on anything it happens to encounter, it is not known whether it feeds on oysters. The question then is: might not *Pycnopodia* be used as a check against *Polynices* in the oyster beds? This could easily be tested out experimentally: *Pycnopodia* could be placed on oyster beds to

see whether it remains there or crawls away. If the latter was found to be the case then *Pycnopodia* is not adapted to feed on oysters and might then be kept on the outside of the oyster beds as a guard against the inroad of *Polynices*.

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THE VIBRATILE ORAL MEMBRANES OF GLAUCOMA SCINTILLANS, EHR.

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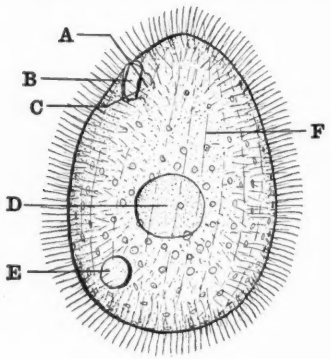
Glaucoma scintillans was first described by Ehrenberg in 1838, and has received since that time but little notice, save as a species to be included in catalogues of microfauna. The writer has found it of interest because of the peculiar appendages borne about the mouth, *i.e.,* the vibratile oral membranes. Other species also bear either one or two oral membranes, but *Glaucoma* is distinct in this respect: that the membranes completely encircle the oral aperture; are distinctly bilabial in form, and are usually in active, characteristic motion. So rapid is the motion of the membranes that, due to the reflection and refraction of the light rays from the microscope mirror which is produced, a twinkling or scintillating appearance results. It is from this phenomenon that the creature has received its specific name, *scintillans.*

The body of *Glaucoma* is ovate (Figs. 1 and 2), the ventral surface flattened and entirely ciliated; the dorsal surface arched, and naked. The cuticle is everywhere longitudinally striated. The oral aperture lies in the anterior half of the ventral surface, its longer axis slightly oblique, though in many individuals the longer oral axis is practically parallel with the longer axis of the body. The nucleus is spherical, its diameter being approximately equal to the long axis of the mouth, and situated in the central portion of the body, often, however, slightly nearer the posterior extremity. A secondary nucleus, roughly a fifth or sixth of the diameter of the primary one, can frequently be made out. The contractile vacuole is usually single, rarely double, and situated in the posterior third of the body. In shape, *Glaucoma* is more constant than many of the other cili-

ates. The adults are usually almost perfectly oval or ovate; the young are apt to be often spherical. In size the adults vary between 70 and 75 microns in length. The writer has noted a few individuals that were 78–80



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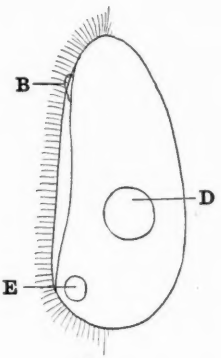

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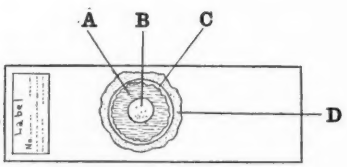

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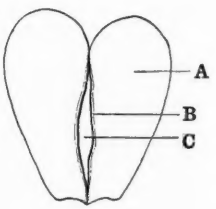

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microns.[1] These, however, were very rare, and did not number more than perhaps a dozen individuals among several hundred.

Glaucoma is a fairly common protozoan. Its usual habitat is in stagnant water, particularly pond water in which there is considerable decaying aquatic vegetation. The writer has found it abundant in the brackish water of a peat swamp. It commonly occurs wherever there are also numbers of small flagellates. Samuelson ('57)[2] says that he has reared large numbers of them in an infusion made from cabbage leaves and distilled water. Cultures of *Glaucoma* were prepared in the laboratory by the writer by allowing water, containing cattails, ponds lily leaves, and *Elodea* to become putrid. Numerous *Glaucomæ* were found congregated in the grayish scum that overspread the surface of the infusions, where they were engaged in feeding upon the bacteria, which seems to form the bulk of their food.

It was necessary to keep individual *Glaucomæ* under observation over extended periods of time, and this was accomplished by means of a device whose utility was such as to warrant a description of it here (Fig. 3). A piece of lens paper, or of thin typewriter manifolding paper,

FIG. 1. Mature *Glaucoma scintillans*, ventral aspect. *A*, indefinite gullet; *B*, vibratile oral membranes or outer lips; *C*, opening to buccal cavity (or mouth proper), or inner lips; *D*, nucleus; *E*, contractile vacuole; *F*, striations of the cuticle.

FIG. 2. Outline drawing of the lateral aspect of *Glaucoma scintillans*. *B*, outer lips; *D*, nucleus; *E*, contractile vacuole. Note that the ventral surface may often be depressed.

FIG. 3. Micro-aquarium. *A*, circle of thin lens paper, bearing a circular opening; *B*, *C*, the cover glass: *D*, sealing material (parafin or Canada balsam).

FIG. 4. The vibratile oral membranes, or outer lips, with the opening of the mouth just beneath them. Semi-diagrammatic.

FIG. 5. The outer lips dissociated from their connection with the cuticle. The broken line represents the position of the surface of the cuticle.

FIG. 6. A single outer lip, showing the transverse striations.

FIG. 7. The outer lips represented as being spread out flat, and seen from above. *A*, outer lips; *B*, inner lips; *C*, opening of mouth proper.

[1] Eyferth (1909) gives the length of *Glaucoma scintillans* as lying between the extremes, 20 and 80 microns! The lesser figure probably refers to the length of the young, just after division.

[2] *Quart. Jour. Mic. Sci.*, Vol. 5, 1857, p. 19.

the shape and size of the cover glass, with a small circular opening cut in its center, is soaked in hot parafin, drained, and placed upon a glass slide. After the parafin has cooled a drop of water containing the organisms is placed in the center of the circular opening, and the cover glass applied. The drop should flatten out just sufficiently to fill completely the space between the cover glass and the slide inside the circular opening. The cover glass must now be sealed down about its edge by means of a camel's hair brush dipped in hot paraffine. Such a device the writer has called a *micro-aquarium* and has found its employment of the utmost use. In it scores of *Glaucomæ* were kept alive for as long as eight hours.

For quieting the movements of *Glaucomæ* thick gelatine solution was used, and a drop, mixed with a drop of water containing the organisms, placed on a slide and examined under the 16 mm. objective and allowed to remain uncovered until evaporation had rendered the mixture of such viscosity as to retard the animals sufficiently. The cover glass was then applied and sealed down with either hot paraffine or castor oil to prevent further evaporation.

For killing without staining and without distortion either a one per cent. aqueous solution of copper sulphate, a ten per cent. solution of alcohol, or a fifteen per cent. solution of chloretone was found satisfactory. The best of all killing reagents for *Glaucoma,* however, was found to be a two per cent. aqueous solution of alum.

Intra-vitam staining was accomplished with an aqueous solution of Bismarck and methyl green; while for staining after killing there were utilized: iodine, methyl green, methyl blue, Bismarck brown, and safranin.

The appendages which make *Glaucoma* of especial interest are the oral membranes. These are present in the form of two hyaline, lip-like structures, lying one on either side of the buccal cvaity (Fig. 1). For convenience these will be referred to as the lips. In form they are roughly rectangular, and approximately twice as

long as broad, with one extremity enlarged and rounded, and the other slightly narrowed and with a crescentric edge (Fig. 4). They are joined at their base, at either end, and project outward from the body so as to be plainly visible in profile (Fig. 2). Usually the lips are in constant motion, but occasionally may be seen inactive, and when so are normally closed (Fig. 1).

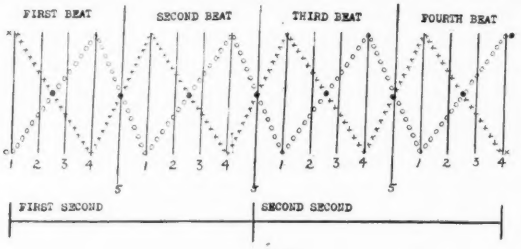
When the body of *Glaucoma* is disintegrated with strong alum solution, or copper sulphate, it is sometimes possible to isolate the two lips together, they apparently being more resistant than the rest of the body. When this is done, it can be seen that they are more nearly oval in outline, possessing an extended, fin-like portion, which projects into, or beneath the cuticle (Figs. 4 and 5).

That the origin of these membranes may be sought for in the fusion of rows of cilia situated on either side of the buccal cavity, is suggested by the fact that each lip exhibits striations running at right angles, or nearly so, to the longitudinal axis (Fig. 6). These striations are broadest at their bases, and narrowest at their tips, and recall to mind the rows of stout oral cilia found among so many of the infusoria.

Between the bases of the lips lies the opening of the buccal cavity, or mouth proper. Its edges, which may be termed the inner lips, are also capable of a motion which will be described later (Fig. 7).

The movement of the outer lips consists of a rapid opening and closing, and is best described by the word, beating. The rate of the beating is apparently under control of the animal, and varies at different times. Under normal conditions the beating of the lips is very rapid. The hyaline membranes, even when at rest, seem to glisten, possibly due to the striations which refract the light in different ways, and when in rapid motion produce the pretty scintillating effect which has given the creature its name. Observations made by the writer of the rate of opening and closing of the lips, showed that it varies from eight or nine times per second, through

all the lessening degrees, to actual cessation. Usually the beating, no matter what the rate, is regular, *i.e.*, the durations of opening and closing being of equal length. This, however, is subject to modification, apparently at will, and individuals are sometimes, though not frequently, encountered in which the lips beat with great



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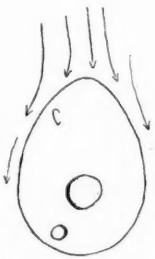

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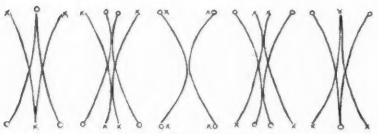

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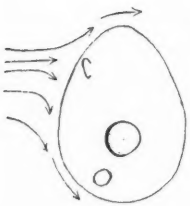

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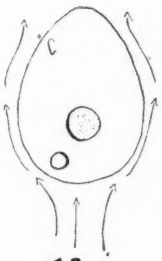

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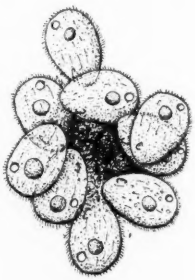

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rapidity for a few seconds, then flutter slowly, then close for a second or two, and then begin slowly to beat again. From experiments which have been made the conclusion is drawn that the rate of the beating of the oral membranes in *Glaucoma* is directly proportional to the strength of the food stimulus received in the buccal cavity, or possibly through the cilia in the region of the mouth.

The lips do not open and close with their ectal edges parallel. The process of closing takes place with a wave-like motion, the anterior edges of the lips meeting first, and the wave of motion thus initiated traveling toward the posterior ends, until, when these finally meet, the anterior edges are open again. The process of opening, therefore, takes place in the reverse direction. Fig. 8 diagrams six stages in a single beat of the lips, and in Fig. 9 are represented four beats analyzed with respect to their cycles of contacts and partings.

The opening and closing of the inner lips, or edges of the mouth proper, take place, apparently, in a similar wave-like manner, and in the reverse order or motion from that of the outer lips. This sequence of motion may aid in forcing food into the buccal cavity, since whenever any given portion of the buccal cavity is open

FIG. 8. Six stages in a cycle of the opening and closing of the outer lips. The edges of the lips are represented diagrammatically to show how the waves of contact and parting follow each other. Stage 7 begins the cycle anew.

FIG. 9. Graphic representation of the relations of the cycles of opening and closing of the outer lips. Four beats are analyzed, each of one half second's duration. The vertical lines represent the line of the outer edges of the lips, and the lines of crosses and circles show how the waves of contact and parting sweep up and down them. Four stages are given for each beat—represented by the four vertical lines of the lips in each beat. The longer vertical lines represent the stages when no part of the lips are in contact. Stages 1, 2, 3, 4, 5, in this figure correspond respectively to stages 1, 2, 4, 5, 6, in Fig. 8.

FIG. 10. Five stages of the cycles of opening and closing of both the outer and inner lips diagrammatically represented, and superimposed to show their reverse relationships. The *o*-lines represent the edges of the outer lips, and the *x* lines the edges of the inner lips.

FIGS. 11, 12, and 13 show the various directions from which water currents, bearing food, can be urged towards an individual by the action of the cilia.

FIG. 14. Group of *Glaucomæ* clustered about a mass of debris and bacteria, feeding.

to receive food, the corresponding portion of the lips above is closed, to force it in. Fig. 10 shows diagrammatically the relationship of the cycles of opening and closing of the outer and inner lips. It will be noted that once during each cycle (at its middle) both the outer and inner lips correspond, for an instant, in attitude, the same portions of each being in contact (Stage 3, Fig. 10). In some individuals the inner lips seemed not to open and close at all, but appear to remain permanently open. Observations on the motions of the lips were made while the animals were incarcerated in very thick gelatine, and all of their movements much retarded.

The ciliary action of the anterior portion of the body can apparently be regulated according to the desires of the animal and water currents, bearing food, can be drawn toward the mouth either from directly in front of the creature, from the side, or from behind (Figs. 11, 12, and 13).

Glaucoma feeds upon minute flagellates and other minute protozoans, fragments of débris, tiny diatoms and desmids, but the bulk of its food seems to consist of bacteria. Fig. 14 shows what may frequently be observed in a culture, *i.e.*, a group of individuals clustered about a mass composed mainly of bacteria, pressing their lips against the substance, and urging portions of it into the buccal cavity by the combined action of the lips, and oral cilia. When feeding in this fashion the movements of the outer lips resembles somewhat the biting and chewing motions of the mouths of the higher animals.

Curiously enough the complex development of the exterior oral appendages seems to have no parallel within the buccal cavity, since neither supporting pharyngeal rods, nor even any definite pharynx, could be discerned.

NOTES ON THE BIONOMICS OF MELLITA[1]

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OBSERVATIONS already recorded[2] led me to devote some attention to the movements and the coloration of *Mellita sexies-perforata*, and to the injuries which are in nature inflicted upon the individuals of this species. The findings incidentally supplement and confirm some deductions made in the notes cited,[2] and serve to indicate several directions in which further study would seem promising.

Mellita lives more or less completely buried in the sand, in channels between islands, at the outlets of sounds, and between the shore and the inner reefs; but always in places where there is a tidal current. The character of the bottom, which may lie 2 to 6 fathoms beneath low water, varies from shell-sand, gray-white and usually muddy, to dark brownish mud. Young and adults of all sizes up to 13 cm. transverse diameter occur in company. The older individuals burrow more deeply than the young ones, the latter frequently lying freely exposed on the surface of the sand. In stormy weather, all the Mellitas dig themselves deep into the mud, to a depth of perhaps 8–9 cm. In the laboratory the older individuals burrow more quickly when exposed to bright sunlight than they do in the dark. Heliotropism, when horizontal light is used, is not precise; younger individuals tend, on the whole, to move away from a source of horizontal light. Normally, light coming from above may be a significant source of stimulation; this was not adequately tested. The low degree of photic irritability toward horizontal light probably accounts for the fact that no photic orientation, strictly speaking, was noted; such orientation might be expected, since the nature of Mellita's locomotion would make it possible.

In locomotion on a solid surface, that part of the body anatomically the anterior is always carried ahead. The "leading"

[1] Contribution from the Bermuda Biological Station for Research, No. 118.

[2] Crozier, W. J., 1918, "On the pigmentation of a Clypeastroid, *Mellita sesquiperforatus* Leske," AMER. NAT., 52, 552–555. 1919, "On Regeneration and the Re-formation of Lunules in *Mellita*," AMER. NAT., 53, 93–96.

point may shift progressively from side to side during an extended act of creeping, but *at all times* some part within the two anterior interradii is in advance. *Mellita* can, however, pivot in complete circles, in either direction, about its mouth as a center; it also carries out successive incomplete swings, alternately opposite in direction. Movements of the latter type, together with the relatively fixed direction of creeping, namely anteriorly, are important for the act of burrowing, and are correlated with some notable growth-changes in the form of the whole body.

During burrowing the anterior end is in advance. The process of concealment is a fairly rapid one, a large specimen being able to disappear completely in less than 15 minutes, although two to three times this interval may be employed. Not only do the spines and tube feet assist in clearing a way through the sand, by moving the individual sand grains, but, in addition, the body as a whole is used as a digging instrument. The disk is repeatedly rotated 30° or more to either side of the sagittal line,

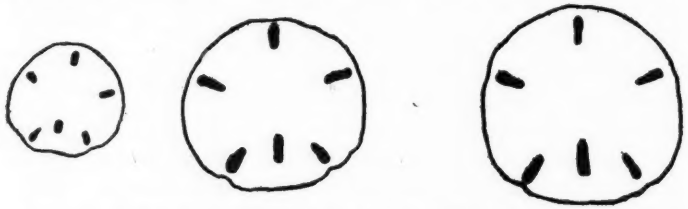
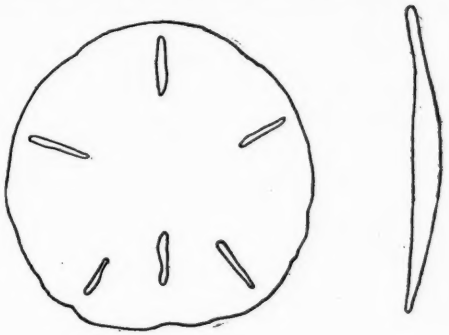


FIG. 1. Outlines of three young *Mellita sexies-perforata*, showing the approximately circular outlines of the body; between the specimens of intermediate and largest size is an antero-posterior section of the former. Attention may be called to the persistence of the marginal notches opposite the two posterior ambulacral lunules, although these lunules, in *M. sexies-perforata*, are formed by the meeting of dorsal and ventral invaginations, not by the inclusion of reëntrant marginal notches—as is the case in other *Mellitas*. (×1.)

with the result that, since the very numerous spines and tube feet are simultaneously pressing the disk forward, the animal is actually insinuated, or "slid," into the ground. This maneuver is especially effective upon a muddy bottom, where movement of sand by the tube feet and spines would be a slow and inefficient process.

The young *Mellita* is quite thin and wafer-like, its outline practically circular (Fig. 1). As the animal grows, the thickness of the body increases, although the edge of the disk remains thin. In many cases the outline of the disk is still almost cir-

cular even in specimens of maximal size, and the ventral surface of the disk practically flat (Fig. 2). It frequently happens, however, that the central region of the body becomes relatively thicker than in the flat, circular sea-plates, and in these individuals there are several noteworthy departures from the typical structure. Anteriorly the disk is more wedge-shaped in vertical



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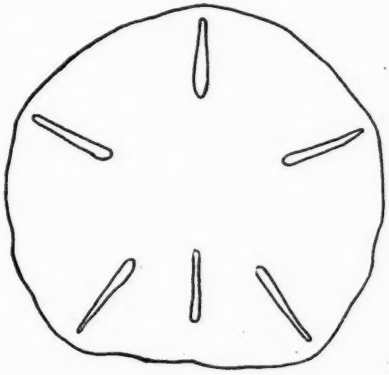
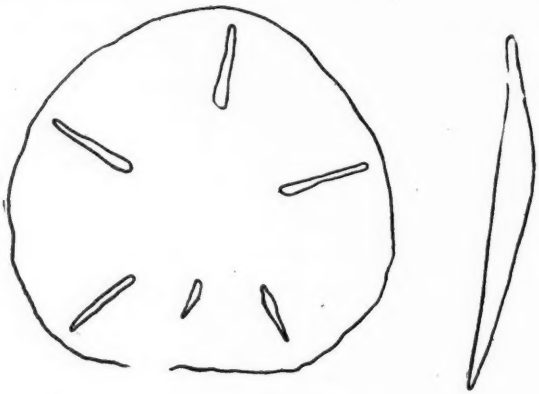


2 b,

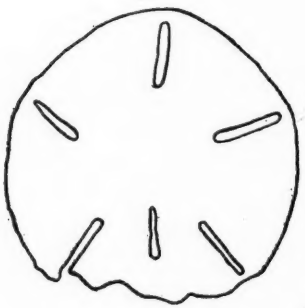
FIG. 2. Outlines of two individuals with circular type of margin, with a sagittal section of one of them (*A*). (× 2½.) In this section, and in the following ones, it will be observed that the anterior margin of the disc is more bluntly rounded than that at the posterior edge—an advantage, presumably, since the burrowing portion of the periphery is thus made stronger.

section; the anterior antimere projects forward, forming a sharp "nose," or entering point, which presumably facilitates burrowing (Fig. 3[4]). The antero-lateral radius on either side

sometimes forms, in addition, a more or less projecting "shoulder" (Fig. 4). These departures from the smoothly circular form, together with the "arched" construction of the test in some older specimens (Fig. 4), derive their effectiveness for



3 a.



3 b.

FIG. 3. Outlines of two individuals with projecting anterior radii, and a sagittal section of one of them. (× ½.)

burrowing from the partial rotation or "swinging" of the disk during this act.

The changes here noted in the form of the body of some individuals with advancing growth, are not detectably correlated with peculiarities of habitat. The different types occur with about the same relative frequency whether the bottom is of shell sand or of brownish mud. The local character of the bottom

changes somewhat, however, from time to time, being more muddy and less sandy in some years than in others. One may nevertheless entertain the idea that genetic factors are concerned in determining the growth-changes in the body-shape of some individuals. This matter should be studied in a larger series of specimens than I have been able to secure in the time devoted to this work. Especially interesting is the fact that this

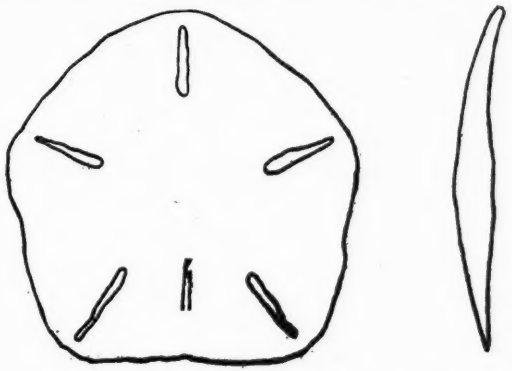


FIG. 4. Outline and sagittal section of a *Mellita* pointed anteriorly and with lateral "shoulders"; the section shows the tendency toward an arching of the test in some of these cases.

species occurs in the fossilized state above the beach zone along the shores of islands in Great Sound. The seven large fossil tests I have examined were all of the almost perfectly circular type (cf. Fig. 1).

In order to follow more precisely the course of growth-changes in *Mellita,* I endeavored to derive the curve of its growth, and to fix the average duration of its life. The results, which are provisional only, are given in Fig. 5. Specimens were measured from one locality—Cobbler's Cut, Spanish Point—in September. The *transverse* diameter was measured, since it is less subject than is the antero-posterior to fluctuations induced (a) by the tendency, already noted, to form a projection at the anterior antimere, and (b) through injuries suffered at the posterior inter-radius. From the modes in the frequency distribution of sizes, it was deduced that at 6-months *M. sexies-perforata* measures 2.2 cm. in transverse diameter; at 1.5 years, 5.7 cm.; and so on, as indicated in Fig. 5. It seems possible that the average duration of life is about 4 years, according with the fact that

the majority of the dead tests, which may be collected in quantity, are about 10 cm. in transverse diameter. From these estimates of age in *Mellita,* the described growth-changes in the form of the body begin to become obvious during the third year of an individual's life; in some specimens they do not occur at all.

During the middle years of its life, *Mellita* has a considerable capacity of withstanding injuries (cf. Fig. 6) and of repairing damage done to the periphery of its body. I have already noted the fact that injured and regenerating individuals are found to have been damaged at the *posterior* end only; the wound illus-

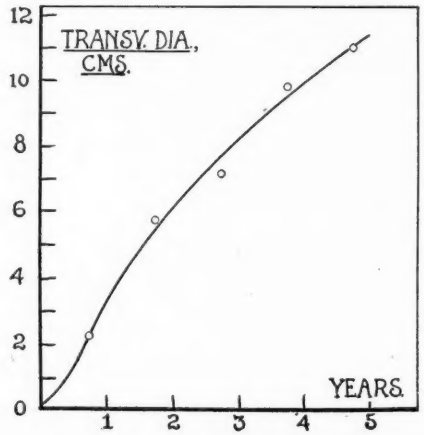


FIG. 5. Possible growth curve of M. *sexies-perforata.*

trated in Fig. 6 is unusually far forward. It was previously suggested (Crozier, 1919) that the posterior incidence of injuries resulted from the circumstance that the posterior end was more freely exposed than the rest of the body. Observations in aquaria and on sand-beaches have shown this explanation to be probably correct. Burrowing takes place with the anterior end in advance, the edge of the posterior inter-ambulacral area frequently remaining exposed long after the rest of the creature has been concealed beneath the sand. The experimental tests were made with active, healthy, specimens exhibiting no green areas upon their surface (cf. Crozier, 1918). During burrowing, the body of the sea-plate is moreover tilted, anterior end down, at an angle of 10°–20° with the surface of the sand; so

that the exposed posterior or postero-lateral margin projects in a not inconspicuous way above the general level of the sand.

In the light of this behavior, and particularly because of the injuries found to have been suffered by the sea-plates, it becomes pertinent to inquire whether an adaptive (concealing) value attaches to the pigmentation of these animals. The occurrence of injured specimens, and that in some degree of frequency (about 60 per cent. of those above 9 cm. transverse diameter), would seem in itself to be valuable evidence upon this point. There are several other important considerations to be derived from the nature of the pigmentation of *Mellita.*

Until it has attained a diameter of 7 to 8 cm., the young *M. sexies-perforata,* seen from above, is practically colorless; the integument contains no pigment, although the yellow-brown stomach may show faintly through the test. Upon attaining this size, a light coffee-tint, evenly distributed upon the dorsum, makes its appearance; previously, at about 5.7 cm. diameter, dark brown pigment begins to show on the *ventral* surface, on each of the polygonal areas surrounded by the tube-foot channels. Pigment thus begins to be deposited on the ventral side; and it continues to be denser (darker) on this side than dorsally. The intensity of pigmentation increases progressively with age, until, in animals on 12–13 cm. diameter, a very dark brown hue is attained.

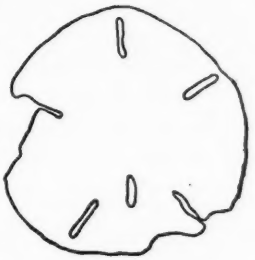


FIG. 6. Illustrating natural injury and initial stages of repair. From the living animal. (× ½.)

M. sexies-perforata, at Bermuda, does not frequent bottoms supporting a good growth of eel-grass. If in other regions it should be found to do so, the alkali-greening substance occurring in this species (Crozier, 1918) and in Clypeastroids generally, might be adaptively concerned in pigmentation. But no green hues are normally evidenced by this species at Bermuda. If the somewhat uncertain records of a green coloration in normal mellitas of this species at more southerly stations are confirmed, and found related to an eel-grass habitat, a direct physical explanation is at hand to account for the greening (cf. Crozier, 1918). The normal brown hue seems due to the integu-

mentary accumulation of some metabolic waste. This view in itself does not preclude the possibility of an adaptive determination of the pigmentation; it would be curious indeed if an internal coloring-matter were not the result of metabolism. In order to remove the possibility of an explanation for the coloration in the customary terms of adaptation, it must be shown that the pigmentation in question is an *unconditioned* result of metabolic processes—unconditioned, that is, by the "need" for concealment and the like. It is, therefore, important to observe that: (1) the degree of pigmentation increases with age; (2) the variously colored individuals live side by side; (3) the tilting of the body exhibited during burrowing, and the exposure of the posterior margin of the body owing to the incompleteness of this act, are not compensated by counter shading—the ventral surface is more darkly colored than the dorsal; and (4), the region known to be differentially exposed in this way is found actually to bear evidence of damage, in a goodly proportion of individuals. The exact origin of these injuries remains obscure, but is not of primary importance here.[3]

The general physiology of pigmentation in the sand-dollars and sea-plates, and the possible evolutionary significance of the growth changes in body-form noted in this paper, should be made the topics of further studies.

DYER ISLAND, BERMUDA, 1918.

[3] I have good reason to believe that the injured mellitas were not damaged as the result of antecedent dredging operations in the same areas.

THE INSECT ENEMIES OF POLYPOROID FUNGI

DR. HARRY B. WEISS
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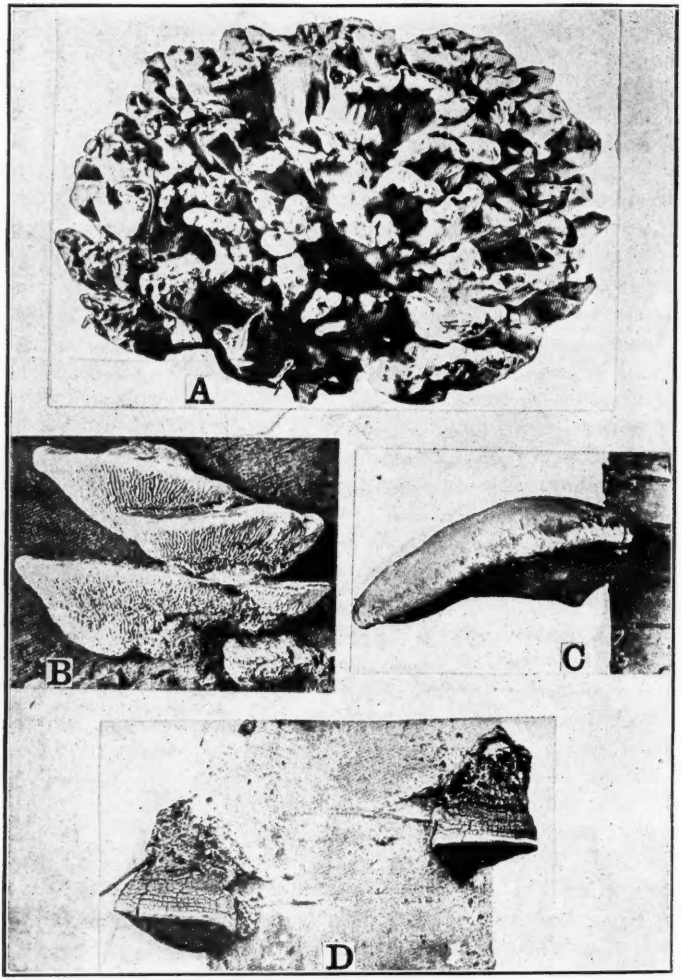
IN the past, entomologists have paid little or no attention to the fungus hosts from which they collected insects, and their captures are usually recorded as having been taken on or in a "fungus." This is a very indefinite term which includes a large number of species and gives no clue whatever as to the identity of the host. Years ago when mycologists were few and far between, it was undoubtedly difficult for entomologists to have the fungi identified but at present this excuse will no longer hold and there is no reason why such hosts should not be specified.

What appears to be a definite relationship between certain fungi or their fruiting bodies and insects has been observed in the past by both entomologists and mycologists. The spores of certain fungi were found to germinate in certain insect burrows and infection in some cases took place through insect apertures. In other cases, certain insects were observed to be present with certain fungi, both on a common host. Whether they acted together, independently, or followed each other in connection with the death of the host is a subject for further study.

The main object of this paper is to call attention to the different groups of insects which are found associated with polyporoid fungi and to urge that the hosts be recorded specifically or as near that as possible so that future workers will be in a position to digest the information intelligently after a large enough mass has accumulated. This paper is really a summary of the observations made during a year's collecting of fungus insects in New Jersey.

The *Polyporaceæ* includes those forms in which "the hymeneal surface is generally spread over the inner surfaces of pores or narrow tubes, sometimes over folds or shallow depressions between vein-like reticulations occasionally more or less lamelloid."[1] The sporophores vary considerably, are often very large and usually tough, and found chiefly on wood in the form of brackets of various sizes and shapes. The members of this family are found on both living and dead wood of deciduous and co-

[1] Duggar, B. M., "Fungous Diseases of Plants."



A. Fruiting bodies of *Polyporus sulphureus.*

B. Sporophores of *Dædalia quercina* on oak railroad tie; rarely attacked by insects.

C. Sporophore of *Polyporus betulinus* on birch.

D. Sporphores of *Fomes igniarius* on aspen.

(All figures after Von Schrenk and Spaulding, Bul. 149, U. S. D. A. Bur. Pl. Indus.)

niferous trees and as a class are very destructive to trees and timber.

New Jersey is not particularly rich in this group, only some 50 species having been found up to the present time and the state has been fairly well collected over. Many of these were taken in what is known as the Piedmont Plain section and while this area is largely under cultivation, it has many large swamp areas and the forests are deciduous. The Pine Barren section of the state was almost devoid of polypores and in the other sections they were found in carying numbers, depending on the size and location of the forested area. Several sections of the Piedmont Plain yielded the most and the species were by far more numerous here than in any of the other sections of the state.

Of the 50 different species of polypores collected 80 per cent. were found to be infested by insects, which were distributed as follows: Of a total number of 74 species, 59 belonged to the Coleoptera, 1 to the Hemiptera, 3 to the Lepidoptera, 5 to the Hymenoptera and 6 to the Diptera. Of the 6 species of Diptera, 2 were crane flies found associated with soft, watery polypores, 3 were fungus gnats and 1 was a member of the *Ortalidæ*. All of the Hymenoptera were parasites of beetles. The 3 species of Lepidoptera belonged to the family *Tineidæ* and the one hemipteron was the flat bug *Aradus similis* found on *Polyporus betulinus* and *Fomes pinicola*. In the Coleoptera 17 families were represented, according to the following table:

COLEOPTERA ASSOCIATED WITH POLYPORES

Family	Number of Species Found on or in Polypores
Hydrophilidæ	1
Staphylinidæ	3
Scaphidiidæ	2
Erotylidæ	4
Mycetophagidæ	3
Dermestidæ	1
Histeridæ	3
Nitidulidæ	6
Trogositidæ	2
Ptinidæ	3
Bostrychidæ	1
Cisidæ	16
Scarabaeidæ	2
Tenebrionidæ	6
Melandryidæ	4
Mordellidæ	1
Anthribidæ	1
	59

With the exception of the species belonging to the *Histeridæ* and part of the *Trogositidæ*, which are predaceous, it is extremely probable that most of the remainder are fungus eaters, as some were taken breeding in and others on or in the fungi. In addition to what might be called the fungus habit of some of the members of the above named families, it might be of interest to note other family habits in a general way and this can be presented best in a tabular form.

OTHER FAMILY HABITS OF COLEOPTERA FOUND IN POLYPORES

Family	General Habits of Members
Hydrophilidæ	Aquatic and terrestrial, found in moist earth, dung, decaying vegetation.
Staphylinidæ	Varied, predaceous, feeders on decayed vegetation.
Scaphidiidæ	Living in rotten wood, gill fungi.
Erotylidæ	In fungoid growths, stems of plants.
Mycetophagidæ	Under bark and in fungus.
Dermestidæ	On dry animal matter and vegetable products.
Histeridæ	Predaceous.
Nitidulidæ	Varied, sap beetles, in fungi or dry animal and vegetable matter.
Trogositidæ	Predaceous, a few in granaries, fungi.
Ptinidæ	On dry animal and vegetable products.
Bostrychidæ	In dry wood.
Cisidæ	In fungi or wood penetrated by fungi.
Scarabaeidæ	Varied, in excrement, decaying vegetation, etc.
Tenebrionidæ	Scavengers, on dead or dry wood, vegetable products, in granaries.
Melandryidæ	In dry vegetable matter.
Mordellidæ	On flowers, dead trees, in plant stems.
Anthribidæ	On dead wood, on fungi.

The members of the *Cisidæ* and *Mycetophagidæ* appear to be the only ones confined almost exclusively to fungi. It is quite probable, however, that such members of the other families as are listed as occurring under bark and in dead wood are feeders on the fungus hyphae which penetrate such places.

Many of the polypores, especially after they have matured, are dry, tough, woody or leathery, although some are soft and watery. In most cases the entire sporophore is consumed by the beetles and their larvæ, or so riddled that it weathers away rapidly. In many instances the partly eaten sporophore affords hibernation quarters for the larvæ or adults during the winter and food the next season until fresh fruiting bodies are produced.

Certain species of polypores appear to be more attractive to insects than others and the following table gives a list of the fungi, together with the numbers of insects in different orders found associated with each fungus.

POLYPORES AND INSECTS FOUND ASSOCIATED WITH THEM

Fungus	Coleoptera No. Species	Lepidoptera No. Species	Diptera No. Species	Hemiptera No. Species	Total
Polyporus squamosus Hud.	1				1
" *brumalis* Pr.	1				1
" *betulinus* Bul.	8			1	9
" *berkleyi* Fr.	11				11
" *sulphureus* Bul.	2	1			3
" *fumosus* Per.	2				2
" *amorphus* Fr.	2				2
" *conchifer* Schw.	1				1
" *tulipiferus* Schw.		1			1
" *pargamenus* Fr.	3				3
" *versicolor* L.	23				23
" *hirsutus* Wf.	5		1		6
" *dichrous* Fr.	4		2		6
" *borealis* Fr.		1			1
" *chioneus* Fr.	2				2
" *albellus* Peck	6		1		7
" *galactinus* Peck	1				1
" *cinnabarinus* Jacq.	3				3
" *lucidus* Leys.	3		1		4
" *curtisi* Berk.	1				1
" *tsugæ* Mur.	3	1	1		5
" *graveolens* Schw.	1				1
" *hispidus* Bul.	1				1
" *gilvus* Schw.	10				10
" *cuticularis* Bul.	4				4
Fomes pinicola Swen.	1			1	2
" *bakeri* Mur.	1				1
" *fomentarius* L.	1				1
" *igniarius* L.	2	1			3
" *lobatus* Schw.	1				1
" *applanatus* Per,	3				3
" *marmoratus*	1				1
Trametes suaveolens L.	1				1
Dædalia unicolor Bul.	1				1
" *confragosa* Bol.	3				3
" *quercina* L.	1				1
Lenzites betulina L.	8	1	2		11
" *sæpiaria* Fr.	2		1		3
Poria Sp.	2				2

From this table it will be seen that *Polyporus versicolor, Polyporus berkleyi, Polyporus betulinus, Polyporus gilvus* and *Lenzites betulina* are all insect favorites, especially *Polyporus versicolor* with 23 species to its credit. Just why these species are so attractive to the Coleoptera is a subject for further study. In fact any discussion at this time of the relationship between insects and fleshy fungi would be unwise on account of a lack of suitable data and the above material has been presented in the hope that it may stimulate interest in a subject which has long been neglected and which contains interesting and perhaps economic possibilities.

SHORTER ARTICLES AND DISCUSSION

NOTES ON THE NEMATODE GENUS CAMALLANUS

RECENTLY a paper by Dr. G. A. MacCallum entitled "Notes on the Genus *Camallanus* and Other Nematodes from Various Hosts" has come to my attention. It is dated July, 1918, and appeared in *Zoopathologica*. I have carefully investigated the date of the paper and find that although it appeared in the July, 1918, number of *Zoopathologica* it was not received at the Library of the Bureau of Animal Industry until August, 1919, and at that time neither the John Crerar, the National Museum Library, the Library of Congress, nor the New York Public Library had received their copies. The Secretary of the New York Zoological Society stated that the edition was sent to Dr. MacCallum, October 14, 1918, and as nearly as I can learn was not mailed out until August, 1919. In a personal letter Dr. MacCallum stated that the paper was "partly issued on July 1, 1918." My paper on *Camallanus americanus* was mailed out on August 13, 1919, and since I can not obtain a definite statement as to the date on which MacCallum's paper was mailed, it is impossible for me to state which paper actually has priority of date. MacCallum's paper was unknown to me at the time my monograph on *C. americanus* (1919) was published; hence it seems that I should discuss the form described by MacCallum, since some of my concepts concerning the genus and its species do not conform with his observations.

In the first place, attention should be called to the fact that MacCallum was undoubtedly misled by the brevity of a preliminary paper by Ward and Magath (1917) into thinking that we believed the two species described were the first from America, as MacCallum asserts. We were well aware of the fact that Leidy (1851) had found the genus, under another name, many years before and had named several species from America. At the time we had many records of it and a great deal of material and, in fact, considered it a common parasite. I have gone over the paper quite carefully and can not see why MacCallum should say that the "general tenor" of our paper implies that the worm is rare.

MacCallum apparently places the genus *Camallanus* in a sub-

family within the family Strongylidæ; I am sorry to disagree with him, however, on fundamentals. He bases his argument on four statements:

1. These worms live in the same organ. However, so do many other worms, trematodes, cestodes, and so forth.

2. They have identical habits and attach themselves to the mucous membrane in the same manner. The true situation is clearly set forth in Looss's (1905) monograph on the hookworm and in my paper on *Camallanus americanus*. Ward (1917) has called attention to the fundamental structural difference in the buccal apparatus of the Strongylidæ and I have pointed out the various methods of attachment to the mucous membrane. The members of the genus *Camallanus* are blood suckers; this may be true of some strongyles, but not of the hookworm. Looss has shown clearly that it is not a blood sucker and gets blood only incidentally as it feeds on the mucous membrane of the host.

3. The muscular pharynx or upper part of the esophagus is essentially the same in both types. This part of the esophagus is the same in all the Myosyringata.

4. The structure of their mouths MacCallum believes to be essentially the same. Ward and I have called attention to the basic fact that the mouths of the strongyles are built up on the circular plan, that they hold fast by suction and then shave off the mucous membrane with additional structures, such as internal cutting plates of the hookworms. In the genus *Camallanus* the mouth is built up on a lateral plan. The valves are in truth jaws and bite; suction is secondary and is produced, as in all Myosyringata, by the action of the esophagus.

It would lead me too far astray to take up all the differences between the families Camallanidæ and Strongylidæ because they even belong in different superfamilies, but I may point out the fact that the former are viviparous forms, while the latter are oviparous, that the Camallanidæ have but one single ovary and the males genital alæ, while in the other family the females have two ovaries and the males have bursæ. These are such important facts in the structure of nematodes that were there no other points of difference, such as the double character of the esophagus in the Camallanidæ, the heavier character of the spicula, and the lack of gubernacula, that they could not be considered in the same subdivision.

I must call the reader's attention to the following points in MacCallum's brief description of the genus *Camallanus:*

1. The length of the worms as given does not embrace enough variation, nor does the recorded width. Worms within this genus have been recorded nearly twice the greatest dimensions which he gives, and mature females have been found much smaller than those which he describes.

2. The ridges in the valves are not always "six main ribs on each side of the central line."

3. My experience is that the worms are dislocated from the mucous membrane with difficulty and that often they are pulled in two or a plug pulled out of the intestine before they can be loosened.

4. I presume that "the bar of chitin across the anterior ends of the median four" ridges is the structure that I have called the anterior wing and its purpose is the attachment of the giant buccal muscles primarily and not for "stiffening them" only, if at all.

5. Certainly not all the males have "three pairs of post-anal papillæ, and one pair of pre-anal." In fact, I am sure that most if not all members of this genus have seven pairs of pre-anal papillæ and five pairs of post-anals, with two para-anal pairs.

6. "The semicircular flap" does not act like a bursa. The action of this structure, correctly called "alæ" has been explained by Magath (1919) and its difference from the action of a true bursa shown.

With regard to the new species; MacCallum identified *C. oxycephalus* from a Mississippi alligator. It is impossible to know whether or not he really had a worm belonging to this species. It would be interesting to know that a species harbored in fishes could live in an alligator. If, as he says, the "general description" from the genus will answer for this species he can not be certain that he had *C. oxycephalus* because there is nothing in his general description that is specific for this worm or any other species.

MacCallum's descriptions of *C. scabræ* and *C. troosti* are so indefinite and meager that either species can not be identified positively from the descriptions and figures. He gives very few measurements and the magnification of the figures is not stated. I had hoped to be able to compare his species with *C. americanus* but I can find no definite data in his paper on which to base the comparison.

The description of *C. chelydræ* is passed over with the state-

ment that "there is no appreciable difference between these and the general description" of the genus which MacCallum states also fits *C. oxycephalus*. The status of this new species seems to me to be doubtful.

MacCallum's basis for describing *C. floridianæ* as new seems to lie in the fact that

> the rods are placed on two levels, one set of four being in front and the other set of four placed behind, and diagonally across the first. Whether this condition is only an exemplification of the way in which they act normally by a sawing motion, I do not know, but this would be reasonable. They may act like a pair of hair clippers and were caught in this position when death took place.

The action which MacCallum assumes is probably not the method of action of these jaws. Since I have previously pointed out the method of action of the jaws, no more needs to be said here on the subject. The criss-cross arrangement of the ridges in the mouth apparatus is well explained on the basis of MacCallum's drawing, which shows that the head of the worm was tilted; I have often seen the same condition in poor mounts of other members of this genus when the heads are twisted a trifle. The appearance is purely an artifact. MacCallum's next point is that this worm has only two parts of the trident present, or that it has, in other words, a bident. The figure does not bear out this assertion; two typical *tridents* are shown, each with three prongs. MacCallum states that the males have six pairs of pre-anal papillæ and three post-anal pairs.

The description of *C. elegans* is quite brief. The author could not determine whether or not the males have one or two spicula, and because the male tail is "not so complete and pretentious as in *C. floridianæ*" he believes that the worms deserve a new name.

In *C. ptychozcondis* the only feature MacCallum noted that seems at all distinctive is the fact that the intestine follows immediately after the muscular esophagus. If this is the case this worm is not a member of the genus *Camallanus*. The anus is on the left of the worm described. If the observation is correct it is the first recorded instance of which I know in the literature on nematodes in which the anus does not lie in the sagittal plane. I am of the opinion that the worm or worms studied were twisted in mounting or handling. Unless a series of sections of this worm can be shown in which the lateral lines are in the same

plane with the anus, I can not accept MacCallum's conclusion. He says "that the vagina has not been seen, but appears to be very near the mouth on the left side." If it were not near the middle of the body and in the mid ventral line I would accept with some caution his conclusion, because this is the characteristic position of the vulvar opening in this genus.

MacCallum's *C. cyathocephalus* is clearly the fourth stage of his *C. scabræ*. I have described in detail this same stage for *C. americanus*.

Unfortunately the description of *C. bungari* is so incomplete and the drawing so obscure that it is impossible to locate the worm even with regard to its genus. Certainly with the slight description given it could not be placed in the genus *Camallanus*, because of the single portion of the esophagus and the type of the oral apparatus. The picture seems to show eggs in the terminal portion of the uterus; if the worm were mature, larvæ only would be found in this portion of the uterus if it belonged to the genus *Camallanus*.

Since I have found *C. americanus* in many different species of turtles in the United States, I have tried to decide whether or not MacCallum found this species and described it as one of his new species. In going over his paper carefully I am unable to admit that from his descriptions and figures he described the worm I recorded under the name *Camallanus americanus*, although it is possible that he might have had the worm. One can not be certain whether or not he had some of the species described by Leidy, nor can one be certain of the validity of any species which he describes.

In the face of these facts it seems to me that at present it would be impossible to accept these species in the genus *Camallanus* and hence I suggest that they be considered as *species inquirendæ*. *Camallanus* is such an important genus that the species described within it should be established without any doubt whatsoever. It is unfortunate that MacCallum did not publish more definite data concerning the forms and it is to be hoped that he will follow up his paper with a complete description of each worm, based on the study of more material and histologic sections.

In the past, nematode descriptions have for the most part been rather superficial and a great deal of confusion has arisen concerning the identification of genera and species. The worms are

so difficult to study on account of the problem of proper technic that it is not surprising that many incomplete descriptions should have been published. It is to be hoped, however, that the day will come when nematodes will be as thoroughly studied and described as other parasitic worms have been and that their classification and identification will be made more certain.

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AN AMICRONUCLEATE RACE OF PARAMECIUM CAUDATUM

PROBABLY no representative of the Protozoa has received more attention in matters relating to life cycles, reproduction, heredity and cytology than has *Paramecium*. It should be of general interest, therefore, to record the occurrence of a race of *Paramecium caudatum* which appears to be entirely devoid of a micronucleus. The recent studies by Dawson (1) on an amicronucleate race or species of *Oxytricha* add interest to the present discovery.

In the fall of 1914 Doctor M. H. Jacobs of this Laboratory used, in certain heat experiments, some *Paramecium caudatum* derived from a culture which exhibited great viability. During the following January Hance (2), in examining some of the sur-

viving *Paramecia,* found that a few were characterized by the presence of three contractile vacuoles instead of two, the normal number. Several of these animals were isolated and became the progenitors of the multivacuolate race studied by Hance (2). In speaking of the cytology of the race Hance mentions the great difficulty experienced in staining the micronucleus and states that "the depression in the macronucleus where the micronucleus usually lies is frequently visible but it appears quite empty." He decided, however, that there was one micronucleus present.

The greater viability and the slightly larger size of this race as compared with the wild races led to its use for class work. Having occasion, during November, 1919, to filter about four hundred cubic centimeters of classroom culture densely populated by this race of *Paramecium* the writer fixed the animals so obtained in warm Schaudinn's sublimate alcohol and subsequently stained them with Delafield's hæmatoxylin. On examination it was discovered that in none of the individuals could a micronucleus be found. This observation in itself was not conclusive since the seeming absence of the micronucleus might have been due to faulty technique. The same material was stained with borax carmine and the absence of the micronucleus as a staining body was confirmed. Later four different fixatives were used and the material stained with Carmalum and in no case was the micronucleus found. Material was then fixed daily from a series of four cultures for periods ranging from two to four months. Throughout this period the character of the *Paramecia* remained constant in that no multivacuolate animal possessed a micronucleus.

For obtaining pure lines of amicronucleate animals with which to make further observations twenty multivacuolate individuals were isolated. Some of the progeny of each of these were stained in aceto-carmine and in each case the micronucleus was absent. The question as to the identity of the multivacuolate race and the amicronucleate race then arose. The fact that the progeny of twenty multivacuolate individuals showed no micronucleus supported this supposition. A number of slides, made before the discovery of the multivacuolate race by Hance, were found in the Laboratory by Doctor D. H. Wenrich, to whom the writer is greatly indebted for his constant interest, valuable advice, and criticism throughout this preliminary work. Both micronucleate and amicronucleate individuals are to be

found on these slides. Several amicronucleate individuals contain three distended contractile vacuoles. All the micronucleate individuals contain only two. There is reason to believe that these slides were made from the same cultures from which Doctor Jacobs obtained his animals for experimentation. Therefore these slides also indicate the identity of the two races. Apparently both the extra vacuoles and the absence of a micronucleus were characters present before the heat experiments referred to.

Throughout the entire history of the cultures observed the lightly stained, comparatively large, very irregular, and expanded macronucleus is characteristic of the race. Under poor cultural conditions animals with regular nuclei are few in number and these nuclei are usually oval in shape and proportionately larger, more lightly stained than others and often blending with the cytoplasm. Under the same conditions condensations of the chromatin material are of frequent occurrence and consist of three types: (*a*) small or large tongues of chromatin, compact and darkly stained throughout or only around the edges, usually lying in a concavity of the macronucleus, (*b*) small, circular, dense masses of chromatin, usually flattened and near the surface of the macronucleus, (*c*) bar-shaped condensations, many times longer than broad, ranging from very loose aggregations of granules to very compact masses.

In the early part of the work the writer often experienced difficulty in deciding whether or not a micronucleus was present because macronuclear condensations frequently resembled micronuclei. But after observing many specimens they were easily distinguishable since neither condensations, lobes, nor detached portions of the macronucleus possessed the detailed structure typical of a micronucleus. They could always be identified on very careful examination as portions of the macronucleus by the arrangement of the chromatin. It is possible that Hance may have seen macronuclear condensations resembling a micronucleus or small detached portions of the macronucleus which at certain times are rather common.

Other differences between the nuclei of micronucleate and amicronucleate animals were noticed. The macronucleus of the wild, micronucleate races is compact, comparatively small and darkly stained with a distinct concavity for the micronucleus. The nucleus of the amicronucleate race is large, expanded, and lightly staining.

In addition to these characters there are also certain other morphological characters which distinguish the race. The amicronucleate race is larger than the wild ones so far observed. The curve of the buccal groove is slightly greater than that of the micronucleate animals. The posterior tip is slightly bent toward the aboral side and the buccal groove itself is shallower since the sides of the groove are bent outward. All evidences so far indicate that the amicronucleate race has the potentiality of forming from three to seven contractile vacuoles.

Attempts have been made by the writer to induce conjugation. A flourishing culture has been allowed to evaporate to half volume and small mass cultures have been submitted to various experimental conditions but so far the writer has been unable to induce conjugation in this race. Hance (2), however, induced conjugation in the multivacuolate race by the method first mentioned. Amicronucleate animals in conjugation are to be found on the slides (made before Hance's discovery of the extra vacuoles) mentioned above. Hence the race has conjugated in the past and attempts will be made to induce conjugation in the future.

The main question in the future study of this race will be the cytology of the conjugation process. This will require experimental work on methods of inducing conjugation in the race and the study of the conjugants so obtained. The effect, if any, of the absence of the micronucleus on the division process will also be observed.

The maintenance of pure lines and the study of the nuclear changes which proceed in ordinary vegetative existence will also be an important part of the future work. If there is a process of endomixis the same means will provide a basis for the study of that phase.

These two matters are the most interesting from the standpoint of cytology, especially since the work of Calkins and Cull (3) on conjugation, and Erdmann and Woodruff (4) on endomixis, in *Paramecium caudatum* show that the active body is the micronucleus and that the macronucleus breaks down and disappears in both processes.

Is the macronucleus affected by different cultural conditions in any definite way and how does the behavior of the nuclei of the micronucleate race compare with the behavior of the macronucleus in the newly discovered race? The preliminary work done so far indicates that there is a definite relation between

environment and the behavior of the macronucleus and that the macronucleus assumes different shapes and appearances under different cultural conditions.

Is this amicronucleate paramecium able to exist indefinitely without conjugation involving a micronucleus and without reorganization of nuclear material, or is there another type of reorganization in this race? A nuclear reorganization, if present, must evidently be of a different type from that described by Erdmann and Woodruff.

These and similar problems are interesting, not only in themselves, but because *Paramecium* has been studied in great detail by Jennings and others with reference to the occurrence of cytoplasmic variations. The amicronucleate race, however, is important because the variation is one of nuclear structure. The importance and interest of the study is increased by the fact that the micronucleus is usually considered to be an aggregation of generative or hereditary chromatin and the body which supposedly initiates reproductive processes of all types and from which, in sexual reproduction, the new nuclei are formed.

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NOTE ON THE OCCURRENCE OF A PROBABLE SEX-LINKED LETHAL FACTOR IN MAMMALS

THE occurrence of sex-linked lethal factors in *Drosophila* is a matter of common knowledge to most biologists. Since mammals have an essentially similar type of sex determination in so far as their dimorphism of sperm is concerned, it is theoretically possible that sex-linked lethal factors should occur among them.

Inasmuch as only a few sex-linked factors of any sort are known in laboratory mammals where numerous other genetic differences have been recorded, breeding tests of linkage relations by ordinary methods are precluded. The first indications of a sex-linked lethal factor would therefore be expected to consist of an abnormal sex ratio at birth and a reduction in the size of litters.

Such conditions are met with in certain Japanese waltzing mice derived from a remarkably closely inbred race. This particular strain of Japanese mice has been inbred from the descendants of a single pair of animals for approximately fourteen years. The animals are difficult to raise and the litters are frequently distinctly smaller than those of non-waltzing mice of inbred races. The great majority of animals of this strain have been bred by Mr. George Lambert of Boston, who has provided adult or young adult animals to the writer for several years. Mr. Lambert is now engaged in recording sex ratio data at the birth of litters and states that at present an excess of females is being produced in his stock. While awaiting increased numerical data from his records, however, it appeared advisable to make a short note of the sex ratio and behavior of this strain in the animals raised under controlled observation.[1] The sex ratio of inbred non-waltzing mice is 103.1 ± 2.8, showing a slight excess of males. The sex ratio obtained from Japanese waltzing race of the Lambert strain is 53.2 ± 5.7. The difference between these ratios is 7.9 times its probable error and is certainly significant.

Since recessive sex-linked lethal factors are transmissible through a female to one half of her male offspring, the sex ratio among the progeny of females carrying sex-linked lethal factors should be theoretically 50.0. Males of the Japanese waltzing race can not, of course, transmit the lethal factor, since if they possessed the factor it would result in their death. If then animals of the Japanese waltzing race are crossed with non-waltzing mice of a race presumably free from lethals, the reciprocal crosses should give markedly different sex ratios. Such is actually the case. Non-waltzing females by Japanese waltzing males should give a sex ratio free from the effect of lethal factors. The observed sex ratio in the F_1 generation of this cross is 118.2

[1] Dr. H. J. Bagg, of the Memorial Hospital, New York City, has kindly placed at my disposal data collected by him while breeding Japanese waltzing mice of the same (Lambert) strain. These data are included with my own in this publication.

± 3.8 and in the F_2 generation 113.3 ± 3.0. The combined ratios are 115.9 ± 2.7. The significant excess of males above that found in the inbred non-waltzing stock is a common result of hybridization. The reciprocal cross gives a most interesting contrast. When Japanese waltzing females are crossed with non-waltzing males the sex ratio is 44.0 ± 7.4. This differs from the sex ratio of the reciprocal cross by 8.9 times the probable error of the difference.

Certain other evidence is obtainable from the results of mating Japanese waltzing females or their female descendants with hybrids of the F_1 or back cross generation. Such crosses give opportunity for a lethal factor to be transmitted and to express itself. We should expect, therefore, that an excess of females would be obtained in the progeny of such crosses. Such is actually the case, the ratio being 78.7 ± 2.9. The exact ratio to be expected would depend upon the numerical relation of young in a given population, obtained from homozygous normal females, to those from females carrying the lethal factor.

The size of litters given by Japanese females irrespective of the sire is distinctly smaller than that of litters from non-waltzing females. The average of 58 litters from Japanese waltzing females is 3.38 and from non-waltzing females (100 litters) 5.93. The litters from Japanese females are therefore .57 times the size of those from non-waltzing females. This result is in general accordance with the presence of a sex-linked lethal factor. x^2 test of the frequency distributions of litters in the two cases shows that the odds are less than one in 1,000,000 that they are the same.

While it is realized that the above evidence is preliminary, its entire consistency and the controlled nature of the material makes it seem likely that *the observed figures indicate the presence of what is apparently the first case of sex-linkage in rodents and of a sex-linked lethal factor in mammals.* The possible exceptions to this statement[2] are to be found in the case of hemophilia recently reviewed by Whitman[3] and in the possible difference in reciprocal crosses between *Epimys rattus* and *Epimys alexandrinus* reported by De l'Isle and reviewed by de Meijere.[4]

[2] Progressive muscular atrophy in man has a lethal action. Its action is, however, so delayed that it seems scarcely to fall into the same category with what have hitherto been considered as sex-linked lethals.

[3] *Jour. Cancer Research*, 1919, 4, 181.

[4] *Archiv. f. Rassengesell. u. Biol.*, 8, 697.

In order to explain the case reported by Whitman an entirely new and unsupported behavior of the lethal factor is hypothesized. This consists in a supposition that females possessing two does of the lethal die. Inasmuch as a female with two doses of a sex-linked lethal could not be formed except by mutation, provided the relations observed in *Drosophila* hold true, the presence of a sex-linked lethal factor of the accepted type does not appear to be strongly supported. In the case of the rats a simple statement of a difference in reciprocal crosses is the sole evidence. In this case no lethal action is apparently involved; but sex-linkage might possibly account for the result. Until actual experimental evidence on this matter is available, however, it seems as though it was not sufficiently definite to be considered as having previously established the existence of sex-linkage in rodents.

C. C. LITTLE

CONCERNING THE FOSSILIZATION OF BLOOD CORPUSCLES

RECENTLY, while studying a series of microscopic preparations of fossil material in connection with paleopathology, I observed in sections of a dinosaur bone (possibly *Apatosaurus*) which I had collected in the Como beds of Wyoming in 1906, some ovoid bodies, arranged around the periphery of vascular spaces and Haversian canals, which looked remarkably like blood corpuscles. Close scrutiny of the available material, however, did not satisfy me that the objects might not be the products or by-products of incomplete crystallization. The majority of the bodies had the size and shape of modern reptilian erythrocytes; the nucleus of course not being evident, since only the outward form of the corpuscle was to be seen. Other bodies, apparently similar, were irregular in shape and hard to distinguish structurally from the regular bodies. These latter, however, may be masses composed of several corpuscles which had become agglutinated.

Not being satisfied with the results of my observations, I should not have published anything about it had I not seen in a memoir by Seitz[1] a description of similar bodies in sections of normal

[1] Adolf Leo Ludwig Seitz, 1907, "Vergleichenden Studien über den mikroskopischen Knochenbau fossiler und rezenter Reptilien und dessen Bedeutung für das Wachstum und Umbildung des Knochengewebes im allgemeinen," *Nova Acta. Abh. der Kaiserl. Leop.-Carol. Deutschen Akad. der Naturforscher. Halle,* Bd. LXXXVII, No. 2, 329–330, Tab. XXI, Fig. 61, where the corpuscles are shown in a photomicrograph in 365 diameters.

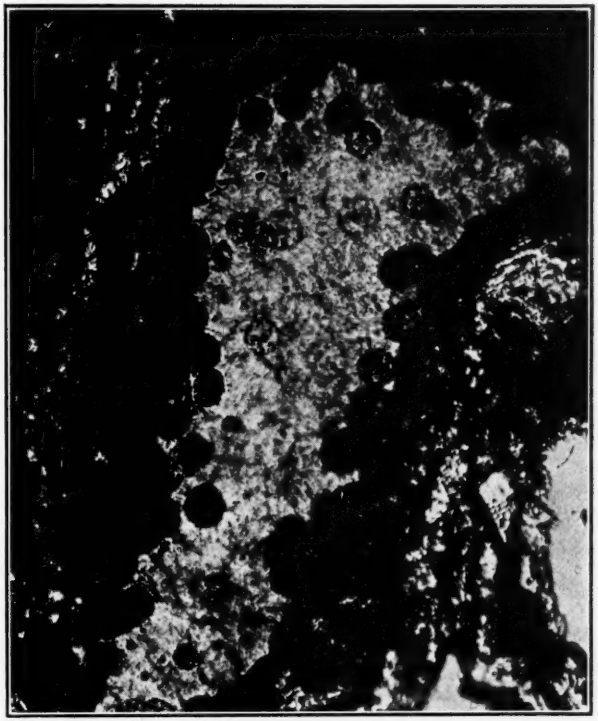

FIG. 1. A vascular space in a normal metatarsal of *Apatosaurus*, or some related dinosaur, from the Como Beds of Wyoming, showing in the rounded marginal bodies, the preservation of supposed blood corpuscles. Magnified 200 diameters. These are the same bodies that Seitz saw in European dinosaurs. The light area is the vascular space filled with clear quartz. The dark marginal areas are osseous trabeculæ rendered dark by iron. The sharp indentations in the border of the vascular space are interpreted by Seitz as Howship's lacunæ, in which case the rounded bodies would be osteoclasts and not blood corpuscles. Renault searched for, but failed to find, blood corpuscles in bone from the Permian of the Autun basin of France.

bone from the European dinosaur, *Iguanodon Bernissaertensis* from the Wealden of Bernissaert, Belgium. Seitz's description of the blood corpuscles follows:

A larger part of the Haversian canals of *Iguanodon* is empty. A part of them, however, contain small, round, biconvex bodies, apparently with flat surfaces, which occur regularly or scattered about in the lumen of the vessels, with an occasional one near the periphery. Not seldom a compact mass of them entirely fills the blood-vessel. Professor Solereder of Erlangen declares that the bodies are not of plant origin

(spores), and by polarization it is determined that the bodies resemble somewhat crystalline concretions, so that we are forced to the conclusion that we have here some fossilized blood corpuscles. The partial filling of the blood vessel may be due to coagulation or a peripheral thrombus. There is also to be found frequent accumulations of reddish crystals which resemble hæmatoid crystals, and which support the suggestion as to the nature of the material. I give these observations with some reservation.

We may gain an insight into the possibility of the fossilization of blood corpuscles by studying the results of the researches into the nature of the mummified brain material of the ancient Egyptians. This subject has been studied by Mair,[2] who finds that the lipoids of the brain from Coptic bodies, 500 B.C., had been changed into cholesteryl stearate and palmitate.[3] Mair obtained cholesteryl stearate by heating cholesterol with stearic acid, and one may infer that the heat of the desert sands in which the bodies were buried may have been an important factor in the conversion of the brain lipoids into the two relatively resistant substances, palmitate and cholesteryl stearate. These brains, even those dating from a period prior to the process of embalming (4500 B.C.), are frequently so well preserved, though greatly shrunken, that practically all the gyri may be accurately determined. This item from more recent times may aid in an explanation of processes occurring in geological ages.

The studies on Egyptian mummies have not resulted in the discovery of blood corpuscles. Schmidt[4] examined bodies dating from 1000 years before Menes (3400 B.C.) to 500 B.C. (mummified material from Coptic bodies) and was unable to find a positive hæmin reaction, tending to show the complete disappearance of all blood in the process of time. Wood Jones,[5] however, is convinced that traces of blood are readily discernible. Elliot Smith has referred to blood stains on bandages used in

[2] W. Mair, 1913, "On the Lipoids of Ancient Egyptian Brains," *J. Path. and Bacteriol.*, XVIII, 179–184; 188.

[3] Mair's results are confirmed and extended by Lapworth and Royle, 1914, "The Lipoids of Ancient Egyptian Brains and the Nature of Cholesteryl Esters, *J. Path and Bacteriol.*, XIX, 474–477.

[4] W. A. Schmidt, 1907, "Chemische und biologische Untersuchungen von ägyptischen Mumienmaterial, nebst Betrachtungen über das Einbalsamierungsverfahren der alten Aegypter," *Ztschr. f. allgem. Physiol.*, VII, 369–392.

[5] F. Wood Jones, 1908, "The Post-mortem Staining of Bone Produced by the Ante-mortem Shedding of Blood," *Brit. Med. J.*, 1, 734–736.

the primitive surgery of Egypt. Ruffer in his extensive studies into the histology of Egyptian mummies did not discover any definite corpuscles.

It may be of interest to note that Friedenthal[6] announced to the physiological society of Berlin the discovery of red blood in the body of a mammoth from eastern Siberia which had been frozen in the tundra since Pleistocene times. The precipitin reaction of the blood is similar to that of the modern elephant. No record is made of the preservation of blood corpuscles. While this is an extremely interesting discovery, it must be recalled that cold brings many chemical reactions to a halt, and there may have been little change in the blood of this mammoth during its 175,000 years of cold storage in the Siberian mud. The body had been so well frozen that the flesh was still fresh enough to satisfy the hunger of wolves and dogs.

Hoppe-Seyler has shown that dried red blood corpuscles of man contain 2.5 parts of cholesterin in 1000. While this is an extremely small amount of lipoid substance, since it is chiefly in the cortex of the corpuscle, it occurred to me that this might offer an explanation of the preservation of blood corpuscles. That is, under favorable conditions, the lipoids of the blood might be changed into some resistant substance like palmitate or cholesteryl stearate and thus retain the form of the corpuscles and delay their destruction long enough for fossilization to set in; these substances being replaced later by the mineral crystals from the magma in which the body was immersed. The beautiful little ganoid fish brains described by the writer[7] some years ago from the Coal Measures may have been preserved in a similar way. The resemblance between brain substance and blood corpuscles is close in this respect that each has a small amount of resistant substance, a large amount of water and a relatively similar proportion of lipoids which may have become transformed, under proper conditions, into resistant substances which carried the part over the critical period of destruction.

In view of the fact that so many soft-bodied animals are so beautifully preserved in the rocks, that the histological nature of Paleozoic muscle tissue has been determined, that bacteria and the delicate parts of flowers are so frequently fossilized, it

[6] *Deutsche Med. Wochenschrift*, 1904, p. 901.

[7] Roy L. Moodie, 1915, "A new Fish Brain from the Coal Measures of Kansas, with a Review of other fossil Brains, *J. Comp. Neurol.*, XXV, No. 2, 135, 17 figs.

is certainly not beyond reason to expect the preservation of blood corpuscles. The subject is still an open one but this contribution to the theory of fossilization, it is hoped, may help to clear up the matter of the preservation of delicate objects.

The fossilization of any of the blood crystals as suggested by Seitz[1] is extremely improbable, since the evanescent nature of the crystals of hæmoglobin is well known. Whether the crystals seen with the supposed blood corpuscles have resulted secondarily from the disintegration of hæmin crystals or whether the whole appearance is due to chemical reactions in the incomplete crystallization of inorganic substances is an open question. Still we must not close our eyes to the possibility of discovery and block the way to progress by saying it is either one or the other. This paper merely opens the field.

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